STOCK STURCTURE AND ENVIRONMENTAL EFFECTS ON YEAR CLASS FORMATION AND POPULATION TRENDS OF PACIFIC HERRING, *CLUPEA PALLASI*, IN PRINCE WIILIAM SOUND, ALASKA

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INFORMATION TO USERS

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Abstract

Fluctuating forage fish populations trigger large ecosystem responses in the North Pacific. A representative species, Pacific herring, *Clupea pallasi*, was chosen to model environmental effects on population fluctuations and recruitment with a case example in Prince William Sound (PWS), Alaska. A unique approach was used to 1) develop a spatially-explicit, life history-based conceptual stock model, 2) quantify population level effects of climatic trends, and 3) model key environmental factors affecting recruitment. Framed as a simulation model, the stock model was compartmentalized by life-history stages based on shared habitats and environmental forcing. Initial model conditions impacting year-class formation were adult size-at-age, spawn timing, location and spawner density, and conditions during egg incubation, all impacting a two-stage larval mortality rate. Larval survival probably dictates the extremes in year-class strength. Age-1 abundance should reflect recruitment levels 2-3 yrs later, unless a predator pit exists. A metapopulation structure was proposed with at least two local population groupings with spatial complexity required to maintain stock levels. Herring abundance correlated with long-term climate trends supporting hypotheses of bottom up environmental forcing. Adult growth was oscillatory over a 13 yr period in phase with zooplankton production and climatic trends. Spawn timing occurred progressively earlier over the last 30 yr period with a concurrent regional spawn allocation shift and decrease in recruits per spawner. Incorporating local stock structure and local environmental variables into nonlinear herring recruitment models improved explanatory power over traditional models. Best-fit variables were eastern PWS SST, salinity, SST variance, and salinity

variance from spring to fall. Eight critical life stage periods were defined based on the season and lag of the best-fitting varibles. Examining other variables in these critical periods led to defining potential key processes affecting year class formation. Allocation of spawn and age-3 recruits to metapopulation regions also impacted recruitment to PWS as a whole and these results supported the metapopulation theory. The results led to formulation of a new theory, entitled "opposing response", explaining the mechanism producing the observed pattern of alternating strong and week year class strengths in northern Pacific herring.

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General Introduction

Pacific herring, *Clupea pallasi*, is an important commercial species and a key forage fish species in the North Pacific due to abundance, commercial value and importance in the marine food chain. In recent times, lack of recruitment and resulting herring population declines in Alaskan waters, particularly Prince William Sound (PWS), is restricting the fisheries. A general lack of forage fish availability including herring (Anderson and Piatt 1997; Bechtol 1997; Anderson et al. 1999) is cited as a possible causal factor in the decline of several sea bird and marine mammal species along the northern Gulf of Alaska (Piatt 1996; Merrick et al. 1997). After nearly a century of commercial fishing activities in Alaska, there is a wealth of knowledge available on Pacific herring. Unfortunately, there is a paucity of information available for other key Alaskan forage fish species, including Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*). Therefore, herring is the species of choice to study causal relationships in long-term fluctuations of forage fish and the marine environment.

Several researchers examined stock-recruitment (S-R) relationships in herring and other forage fish species including the role and scale of environmental factors regulating Pacific herring recruitment (Taylor 1963; Schweigert 1995 and 1996; Ware 1995a & b; Zebdi and Collie 1995; Zheng 1996, 1997). The large cyclic population fluctuations in clupeoids are indications of forcing by density-independent processes (Cushing 1982) that may over ride S-R relationships. Patterns in recruitment trends have been compared

across geographic regions within the North Pacific and between the North Pacific and North Atlantic (Zheng 1996, 1997; Williams and Quinn 2000a, 2000b). These studies provide clues about the scale of the environmental forcing factors.

In general, S-R relationships vary among species and geographic region. Within a given genus or species, a S-R relationship may be very clear in one region and non-existent in another. Northern anchovy (*Engraulis mordax*) exhibit a poor S-R relationship while Peruvian anchovy (*Engraulis ringens*) exhibit a strong relationship (Zheng 1997). In contrast, the Pacific sardine (*Sardinops sagax*) population in California shows a clear relationship while a more southern population in Chile does not. Atlantic herring (*Clupea harengus*) show stronger S-R relationships than Pacific herring (Zheng 1996, 1997). Among Pacific herring populations, some areas exhibit significant but weak S-R relationships (Eastern Bering Sea and British Columbia) and other areas appear to have no relationship at all (PWS and Sitka Sound; Zheng, 1996). A large degree of variability in Sitka recruitment is explained only when sea surface temperature (SST) and upwelling are included in the S-R model (Zebdi and Collie 1995). The inclusion of wind-driven transport and SST improves a S-R model for the Bering Sea (Wespestad 1991). Best-fitting and region-specific NE Pacific and Bering Sea S-R models with environmental variables always include SST and upwelling, and often include climate indices (especially the southern oscillation index) and air temperature (Williams and Quinn, 2000b). Environmental factors probably play a bigger role in regulating Pacific herring recruitment than Atlantic herring (Zheng1996, 1997). Environmental processes affecting recruitment occur at basin- or meso-scale levels with dissimilarities among populations

increasing with distance (Zheng 1996, 1997) and latitudinal groupings evident (Williams and Quinn 2000a). Clearly, forage fish S-R relationships and the role of the environment in the regulation of long-term population trends must be examined on an individual species and region approach because of the large amount of variation among species and regions.

Most studies examining environmental effects on Pacific herring recruitment use factors representing atmospheric or oceanic conditions over broad areas (Schweigert 1995; Zebdi and Collie 1995; Williams and Quinn 2000b). While the environment-herring relationships discovered provide insight and some predictive capability of long-term trends, they contribute little to understanding true mechanistic processes in operation (Williams and Quinn 2000b). Although S-R function fits improve with the addition of these large-scale factors, the proportion of recruitment variation explained rarely exceeds 70% and is generally closer to 50%. Herring recruitment and survival model fits improve with inclusion of localized factors that are thought to have direct impacts on growth and survival, as in a British Columbia study where Fraser River discharge, hake (a herring predator) biomass, the presence of sardines (a competitor), and SST were included (Schweigert 1995; Ware 1995a). The inclusion of smaller scale, life-stage specific regional forcing variables probably improves recruitment models because they directly affect or are more closely related to the mechanistic processes operating than are climatic parameters. Smaller scale environmental variables also may aid in detecting and predicting spatial structure within a given population. Indeed, discrete

herring stocks are often defined by their spatial distribution and hydrographic features associated with one or more spawning areas (Cushing, 1967; Sinclair, 1988).

For this study, PWS, Alaska, situated in the Northern Gulf of Alaska, is selected as the site for a unique, localized approach to recruitment modeling and stock structure formulation. The first objective is to develop a conceptual stock model based on temporally- and spatially-explicit life history characteristics. The second objective is to gain a better understanding of key environmental factors and mechanistic processes regulating Pacific herring year-class formation and other life history parameters. To accomplish the objectives, the tasks needed are:

1. Adopt population theory that is most applicable to PWS herring;
2. Formulate a PWS conceptual model, based on the adopted theory, using literature based and observed concepts and parameters along with observed and hypothetical spatial and temporal distribution patterns;
3. Formulate testable hypotheses, from the model, concerning PWS stock structure, population cycles and processes affecting year-class formation;
4. Analyze the effects of spawn distribution and environmental factors, at a variety of temporal and spatial scales, on magnitude and allocation of recruitment among regions in PWS;
5. Derive conclusions from the analytical results used to test the hypotheses, and formulate new theories and conclusions concerning stock structure and key factors controlling year-class formation.

This study comprises three chapter components and a summary. In Chapter 1, I formulate the conceptual stock model and hypotheses for PWS herring (tasks 1-3). In Chapter 2, I analyze the effects of climate, zooplankton production, and long-term changes in spawn distribution on smoothed, long-term trends in population size, size-at-age, and herring production (tasks 4 and 5 in part). In Chapter 3, I examine the possible causes of extreme variability in recruitment leading to the short-term "noise" in the PWS population trend rather than examining the effects of climate over the smoothed long-term series. I also examine spatially explicit patterns that help test hypotheses concerning stock structure (tasks 4 and 5). Finally, I provide a summary and conclusion of the previous three Chapters and pose a new theory about mechanistic control for year-class formation (task 5).

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Chapter 1. A life history approach to defining herring stock structure[1]

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Abstract

A life history-based conceptual model of Pacific herring stock structure was formulated using existing knowledge about herring. The purpose of the model was to synthesize life history information in a functional form and to use that synthesis to extrapolate a spatially dynamic stock structure. Framed as a simulation model, the form was spatially explicit, dynamic and ecologically based. In a given population, variability of life history parameters was hypothesized to be life-stage specific depending on the number and spacing of patches or aggregations of individuals, within-patch density, the ratio of reactive patch scale to the scale of environmental variability, and the magnitude of environmental forcing. The model was compartmentalized into four, overlapping life-history stages by shared or similar habitats, types of environmental forcing factors, and scale of forcing: adult, embryo, larval, and juvenile. Flow between life-history stages was expressed in numbers, size, and time-varying energy density. The appropriate model unit was a related group of aggregations, drifting, rearing, or spawning together. Model variability was influenced by spatial and temporal scale of environmental variability. Key factors for year-class formation were hypothesized to be adult size-at-age, spawn timing, location and spawner density, conditions during egg incubation, a high two-stage larval mortality rate. Anomalously high or low year classes probably reflect very high or low larval survival. By age-1, abundance should be directly correlated with year-class strength 2 and 3 yrs later unless the local population is in a predator pit. From the model and region-specific information, a Prince William Sound metapopulation stock structure is proposed comprising two (Eastern and Southwestern), possibly three (Northern), major

local population groupings each possessing unique adaptive strategies for successful recruitment.

Introduction

Ecological models are being used with increasing frequency for marine fish to help visualize, understand, and predict complex processes that possess temporal and spatial components (Giske et al. 1998; Hofmann and Lascara 1998; Whipple et al. 2000). Ecological models have been applied in understanding recruitment and distribution of herring and other small schooling pelagic fish (e.g. Jovellanos and Gaskin 1983; Campbell and Graham 1991; Fisken et al. 1995). Models do not generally include all life history stages nor are they commonly applied to answer stock structure questions. During year-class formation in fishes, processes occurring in early life history stages can have cumulative or continuing affects in later stages (Cushing 1975; Bakun 1996). Therefore, a dynamic simulation model with representations of sequential life history stages or periods is useful in conceptualizing year-class formation (e.g. Rosland and Giske 1997). The incorporation of habitat selection theory (Fretwell and Lucas 1970; MacCall 1990) and modern thinking on herring stock structure (McQuinn 1997) are useful to guiding spatial aspects of a conceptual model (Fernö et al. 1998).

A conceptual, life-history based stock model is presented summarizing observed and modeled life-stage specific processes regulating survival, year-class formation, and distribution of Pacific herring, *Clupea pallasi*. Framed as a simulation model, the form is spatially explicit, dynamic and ecologically based. Testable hypotheses are proposed based on model components. Therefore, fully parameterized, the model may be useful in

testing process oriented and stage-specific hypotheses. Using the conceptual model, observed temporal events, and observed and modeled spatial distributions, a stock structure is proposed for the Prince William Sound (PWS), Alaska herring population based on metapopulation theory (Levins 1968).

This study has implications for fisheries management and future research of herring in PWS. Currently, PWS herring are managed as a single stock (Baker et al. 1991). There is no policy protecting individual and potentially separate spawning groups or sub-stocks. If spatial stock structure exists, there is a potential for overfishing a particular spawning group. Fishing changes spawning areas resulting in an overall decrease in population fitness (Wespestad, 1991; Stephenson, 1999). Stock complexity should be preserved via the protection of spawn site diversity (Hay and McCarter 1991; Stephenson 1999). Issues of spatial biocomplexity and population theory are reviewed here and applied in the context of PWS. These results could be used as justification for conservative management practices that preserve biocomplexity and overall population fitness.

Data Synthesis and the Conceptual Model

Information summarized for the conceptual model includes Atlantic herring (*Clupea harengus*) and Pacific herring as many concepts apply to both. Literature on other fish species is included if the concepts also apply to herring. The literature base on Atlantic herring is extensive dating back to the late 1800s (Sinclair 1988). There is a large literature base on Pacific herring with considerable information about adults and embryos, some concerning larvae, and a small amount on juveniles. The development of

widely spread Pacific herring reduction fisheries in the early 1900s resulted in the first reservoir of knowledge (Rounsefell 1929; Taylor 1964; Reid 1971). From the 1930s to the present, the vast majority of studies were done in British Columbia (BC) by the Canadian Department of Fisheries and Oceans (DFO; Stocker 1993). For a ten year period following the 1989 *Exxon Valdez* Oil Spill (EVOS), a large body of knowledge on all life stages was compiled from PWS for the purposes of damage assessment and restoration (Brown, et al., 1996; Marty et al. 1999;). The Sound Ecosystem Assessment (SEA) study, an EVOS research project, was ecologically oriented to examine processes involved in juvenile herring survival (Norcross et al. 2001). Therefore, PWS (Figure 1) has been selected as the case example for this paper. However, many of the concepts outlined here generally apply to Pacific herring and, to a lesser extent, Atlantic herring and marine forage fishes with similar life histories.

In formulating a conceptual model, it is useful to compartmentalize temporal life history stages into groups by shared or similar habitats and environmental forcing. Life history stages and stage-specific habitats of Pacific herring are represented in Figure 2. The times listed are specific to PWS and would be different for other Pacific populations. The life stages have been grouped into four overlapping sub-models; the input of one is the output of the preceding one. Each sub-model represents a functional unit that can be a specific aggregation or a local population. The adult sub-model begins with the number of age 2.5 immature adult recruits and ends with the number of embryos produced from sexually mature adults, that begins at age 3 for PWS. The embryo sub-model includes sessile embryos through drifting post-hatch larvae. The larval sub-model spans from post-

hatch through metamorphosis. The final sub-model is the juvenile stage. Ages of fish stated in the model are determined from the spawning date of the particular cohort occurring in April in PWS (Funk 1995).

The sub-models comprise state variables representing abundance at each stage, flows representing survival between stages, flow regulators representing processes directly affecting survival, and flow modifiers representing processes influencing regulators or influenced by abundance (density dependence). The direction of the arrows indicates the direction of influence.

For herring, the flow between sub-models is most appropriately expressed as numbers and energetic content due to the survival strategy. The inputs and outputs are expressed in numbers of individuals; however, a size- and energy-by-weight distribution accompanies each transfer and energy density is allowed to vary over time so that energetic currency can be used in the model. A life history strategy for herring is seasonally varying storage of lipid reserves in preparation for fasting periods and reproduction (Blaxter et al. 1982; Paul et al. 1996). For the model, energy density is assumed to be approximately a function of weight (Arrhenius 1995; Rosland and Giske 1997) at a given season and age (Paul and Paul 1998). A time and average horizontal location for individuals in the group also accompany each input.

Spatial scale of environmental forcing, stage-specific reactive distance, and the aggregation characteristics of a particular fish species are important considerations for ecosystem-approach modeling (Hofmann and Lascara 1998). In a given population, the scale of spatial variability in life history traits is explained by ontogenic variation in

habitat selection range (Werner and Hall 1988; Higgs and Fuiman 1998). Fish aggregations with overlapping reactive volumes are called a patch, which is therefore the probable unit of spatial variation for herring (Fernö et al. 1998). If spacing between patches is large, inter-patch variability of growth and survival may be high reflecting differences in average individual size, within-patch density, food availability, predator risk, and temperature. Reactive volume is small for larvae (Higgs and Fuiman 1998) and large for adults (MacCall 1990), however, the scale of identifiable environmental forcing may be apparent for a patch rather than an individual. I therefore propose that in a given population, variability of life history parameters will be life-stage specific and depend on the number and spacing of patches, the within-patch density, the ratio of the reactive patch scale to the scale of environmental variability, and the magnitude of environmental forcing. For example, if the reactive range of a larval patch is 0.005 km^3 but environmental variability within the retention region varies on the order of 1- 2 km^3, growth and survival rate differences between patches may depend solely on differences between patch-specific larval weights and densities. In contrast, the reactive volume of juveniles may be on the order of 1.8 km^3 (based on the size of a herring nursery bay in PWS) and similar to the scale of variability in the nearshore nursery habitat. Therefore, inter-patch variability in juveniles may be high, especially if conditions among nursery sites vary considerably. Growth and survival rates probably change abruptly at life history break points, such as hatch or metamorphosis, when patch distribution range changes. As distribution range increases with ontogeny, population level growth and survival rates should express increasing variability.

The Adult Sub-Model

Adults are highly migratory (Winters 1977; Sinclair and Iles 1985; Stocker 1993; McQuinn 1997) over small or large regions. In the spring, Pacific herring concentrate in dense aggregations in shallow water and spawn at population-specific beaches (Hay and McCarter 1997). Pacific and Atlantic herring spend summers broadly distributed in loose aggregations, generally where zooplankton are abundant (Blaxter et al. 1982; Sinclair 1988; Hay and McCarter 1997). In the fall, Pacific herring migrate to population-specific overwintering areas generally in nearshore waters less than 100 m in depth (Hay and McCarter 1997). The range of Pacific herring summer feeding area is associated with the available shelf area (< 200 m deep) and population size is approximately correlated with the size and carrying capacity of a particular shelf region (Hay and McCarter 1997).

Modeling of a specific population requires region-specific knowledge of its distribution. In PWS, historic fishery catches from the early 1900s (Rounsefell and Dahlgren 1932; Skud, et al., 1960; Reid, 1971) and recent research both provide similar evidence of the broad summer distribution of adult herring. There are concentrations in SW PWS (Stokesbury et al. 1999a) and Southern PWS near passes (Norcross et al. 2001) to the Gulf of Alaska (GOA) (Figure 3). In PWS, herring begin to aggregate at known overwintering locations in October (Figure 4; Donaldson, et al., 1994; Stokesbury et al. 1999a). By late March, the PWS overwintering period ends as the spawning migration commences. The majority of spawning occurs in April (Brady 1987; Biggs et al. 1992). The major spawning areas in PWS (Figure 1) have been well documented since the 1970s in PWS (Biggs et al. 1992; Donaldson et al. 1994). Although not as well documented,

small amounts of localized spawning have been observed well into June (Biggs et al. 1992; Stokesbury et al. 1999a, Brown et al. 2003) that may have an important effect on structuring small local populations (Stocker 1993).

For herring, spawning-site fidelity and the processes governing it are key factors for the integrity of a local population (Sinclair 1988). Understanding these factors is important for selecting the appropriate population unit to model. Both Atlantic and Pacific herring show a large degree of fidelity (75-95%) returning to spawn repeatedly in the same regions (Hourston 1982; Blaxter 1985; Wheeler and Winters 1984; McQuinn 1997; Hay et al. 1999). Unlike salmon, Pacific herring show variability in exact site selection (Haegele and Schweigert 1985). Pacific herring fidelity rate is scale dependent and varies with time at sea (Hay et al. 1999). For the major migratory stocks of BC, herring fidelity is highest (82% for 1 yr at large and 78% for 2 yrs) in regions ranging from 10-30,000 km^2 and including up to 4000 km of shoreline as compared (50-60%) to areas about $1/10^{th}$ the size of regions (Hay et al. 1999). There are small, non-migratory stocks that never leave an area and show high fidelity to a small area, such as a particular inlet. However, it is unclear how these stocks maintain their integrity since migratory and non-migratory herring often mix for at least part of the year. Hay et al. (1999) concluded that maintenance of stock integrity occurs only through separation of spawning in place and/or time and stressed the need for better genetic data. Herring are probably locating spawning sites based on a combination of genetics, learning, and reactive mechanisms, such as memory-based state-location comparisons and orientation to gradients in the sea (Fernö et al. 1998) rather than precise chemical imprinting used by salmon (McQuinn

1997). Juveniles follow and, therefore learn from adults, areas favorable for feeding, overwintering, and spawning and thus perpetuate a local spawning unit (McQuinn 1997). Homing for Pacific herring may be an "aggregation" characteristic and is therefore not firmly established until the first spawning or maturation (Hourston 1982).

The main regulator of flow in the adult sub-model (Figure 5) is mortality probably due to predation, fishing, and disease. Mortality rates are modified by predator abundance, exploitation rates, pollution, and herring density. Mortality therefore may be higher when herring aggregate in dense schools during the winter and spring. In PWS, humpback whale predation can be particularly intense on overwintering herring aggregations (J. Wilcock, ADFG, personal communications). Predation is intense during spawning, and a host of species from gulls and sea ducks to sea lions and whales accompany the spawning migration. Disease is facilitated by density and stress (Marty et al. 1999). Poor fish condition, added to the stress of spawning (Carls et al. 1998, 2001), facilitated the massive outbreak of Viral Hemorrhagic Septicemia Virus (VHSV) in April, 1993 in PWS (Meyers, et al., 1994). The outbreak reduced the adult population by 75% (Funk, 1995). Smaller scale VHSV episodes occurred in 1997 and 1998 in PWS with over 10% of the spawning population infected. However, since then, infection rate has remained at less than 2% probably reflecting a baseline rate (G. Marty, University of California Davis, personal communication). Winter also may be a likely period of outbreak, when they are densely aggregated and in a weakened state from fasting (Paul et al. 1996). Pollution can stress fish and induce disease. In an experimental setting, oil exposure increased individual stress and induced the expression of VHSV (Carls et al.

1998). Based on histopathological comparison of PWS adults, one group exposed during the Exxon Valdez Oil Spill (EVOS; Marty et al. 1999) and another exposed to adults to oil in the laboratory, Carls et al. (1998) concluded that a VHSV outbreak probably occurred in 1989 following EVOS. In PWS, pollution may have lowered predation from removals by avian predation since thousands of sea birds and marine mammals herring predators were directly killed by oil in 1989 (Spies et al. 1996). However, predation rates on herring actually may have been higher, because of the weakened condition of herring, and may have compensated the predator removals.

Growth and condition become important modifiers of predation and disease if mortality rates are condition dependent (Figure 5). Growth is the direct result of food and temperature (Lasker 1985). However, predator avoidance may impact feeding rates (Hugie and Dill 1994) and herring have probably adopted a dusk and dawn feeding strategy to minimize visual contact with predators (Blaxter et al. 1982). Adult herring feed opportunistically on a variety of plankton, especially large species (Blaxter, 1985). Growth in PWS adults is not density-dependent but rather is in phase with climate indices and climate-induced zooplankton production (see Chapter 2, this dissertation). Growth is weakly density-dependent in Sitka Sound (Collie 1991; Figure 1) and density-independent, with mainly temperature regulation, in Newfoundland Atlantic herring (Moores and Winters 1982).

The output of the adult sub-model is numbers of embryos produced. The main regulators of output are size-dependent fecundity and egg retention that are in turn modified by spawn timing, adult growth and condition, size composition, and pollution

(Figure 5). Sexual maturity is size-dependent (Hay and Brett 1988), size-at-age varies regionally, and thus age at first spawning is region-specific. In PWS, a proportion of the age-3 cohort spawn for their first time (Funk, 1995), compared to age-2 in BC (Hay 1985), and the proportion spawning depends on average individual fish size within the cohort. Growth and condition previous to spawning modify reproductive processes indirectly through affects on lipid reserves needed to produce eggs (Tanasichuk and Ware 1987; Hay and Brett, 1988; Winters, et al., 1993; Winters and Wheeler, 1996). The winter temperature exposure history of Pacific herring females results in a trade-off between fecundity and egg size with more, but smaller, eggs produced in warmer temperatures (Tanasichuk and Ware 1987). Spawn timing is a modifier of fecundity and is a function of age composition since older, larger Pacific herring spawn earlier (Ware and Tanasichuk, 1989; Hay, 1985). Spawn timing is modified by the temperature exposure history of adult Pacific herring (see Chapter 3, this dissertation; Hay, 1985; Hay and Kronlund 1987; Ware and Tanasichuk 1989; Wespestad 1991).

Herring exhibit maturation and spawn timing plasticity and can thereby modify reproductive activities to optimize larval retention and environmental conditions during larval emergence (Sinclair and Tremblay 1984; Winters and Wheeler 1996). Atlantic herring show a similar plasticity in maturation and spawn timing related to adult size composition and condition in the fall and January sea surface temperature (SST; Winters and Wheeler 1996). As in other Pacific populations, PWS herring spawn timing is relatively variable with a mean date on 20 April ± 12.3 days and a duration spanning 11 to 44 d with a mean of 25 d (Biggs et al. 1992; J. Wilcock, ADFG, personal

communication). PWS Herring may have adapted April spawn timing to correspond with peak copepod blooms (Cooney et al. 2001) and lower flushing rates (Royer, et al., 1990) thus maximizing larval retention after hatch. Adaptive modifications of spawn timing that affect larval hatch timing should generally have a compensatory affect on larval survival. This compensatory effect may have resulted in a lack of observed influence of spawn timing on the ultimate survival of the year class in the Bering Sea (Wespestad 1991).

Spawn timing, embryo lipid reserves, spawning location, egg density, and pollution are the modifiers that carry forward to the embryo sub-model and provide the "initial conditions" for embryonic and larval survival (Figures 5 and 6). Spawner density and spawn timing modify egg density and pollution can affect spawn timing and cause reproductive impairment. Stress from hydrocarbon exposure can induce premature spawning (Struhsaker, et al., 1974). Oil is lipophilic and exposure of adult spawners results in reduced larval viability at hatch (Kocan et al. 1996b; Carls et al. 1998). In PWS, large variations of spawner density cause variations in egg density at similar magnitudes (Willette et al. 1998). Spawner density can be a function of size of pre-spawning aggregations, SST exposure history, and tidal velocity at the spawning site (Hay, 1985; Hay and Kronlund 1987). More importantly, spawner density directly affects egg density, a direct modifier of embryo survival rates (Figure 5; Palsson 1984; Rooper et al., 1996).

During the adult stage, the main impacts on year-class formation originate in processes affecting reproductive rates, egg size, and characteristics of spawn deposition that carry on to future stages. Additional parameters could be added to existing models of egg to post-hatch survival (McGurk et al. 1990; McGurk and Brown 1996) to test for

effects from processes during the adult reproductive stage. Validation of such a model would require site-specific larval sampling. Spatial-explicit models of habitat selection for pelagic fish that aggregate(Fiksen et al. 1995; Rosland and Giske 1997; Fernö et al. 1998; Maravelius 1999) may be useful as they allow for non-optimal adaptive choices related to reproduction. However, modifications are needed for longer lived species such as herring (Fiksen et al. 1995; Rosland and Giske 1997) and for size-structuring within aggregations (e.g. Hughes and Grand 2000).

The population-level hypothesis generated from this sub-model is:

H_n1. Population size is event-driven and determined by mainly top-down events such as disease outbreaks, increases in large predators (e.g. whales or sharks) or anthropogenic causes (e.g.overfishing, oil spills).

Alternative H1 (not represented in sub-model): Population level is determined by an accumulation of bottom-up forcing and is mainly climate-driven.

The process-oriented hypotheses generated from the from the adult sub-model are:

H_n2. Predation is a major source of adult removals but is relatively constant.

Alternative H2. Adult size- and condition-dependent predation (non-human) is the main source of annual adult removals and is modified by predator population sizes and spatial overlap with predators.

Corollary H2.1. Predation is stage-specific; spawner density affects predation levels during the spring.

H_n3 Adult growth and condition is not density-dependent and is dictated by food availability and ocean temperature in the upper 100 m.

Alternative H3. Adult growth is density-dependent and further modified by food availability and ocean temperature.

H_n4. Size-at-age of adults and behavioral choices during reproduction (e.g. spawn timing, and spawn location) are not related to year-class size.

Corollary $H_n4.1$. Stock-specific spawn timing is determined by age composition alone.

Alternative H4. Spawn timing impacts recruitment and is stock specific, adapted to optimize larval retention and survival with variability induced by adult size-at-age and local environmental conditions.

Corollary H4.1. Spawn timing is modified by age composition, individual condition, exposure history of temperature (< 12 mo), current hydrographic conditions, and pollution can induce early spawning.

Corollary H4.2. Environmental factors affecting size-at-age and behavioral choices of adults during reproduction also affect year-class formation, evident as correlations between year-class strength and factors occurring a year or more prior to spawning (cohort year).

H_n5. Spawner density is determined solely by local population size.

Alternative H5. Spawner density is determined by local population size and local hydrographic conditions.

Hn6. Fecundity and egg retention are solely a function of body size and condition.

Alternative H6. Fecundity and egg retention rates are determined by the size and condition of the females, temperature exposure history, local hydrographic conditions during spawning, pollution, and spawn timing.

Hn7. Egg density is solely a function of spawner density.

Alternative H7. Egg density is a function of spawner density and spawn timing, both influenced by local hydrographic conditions.

H_n8. Embryo lipid reserves are a function of egg size, which is a function of fecundity and temperature exposure history of the adult females.

Alternative H8. No alternative is proposed since the null hypothesis has been accepted (Tanasichuk and Ware 1987)

The Embryo Sub-Model

The number of embryos and the modifiers carried over from the adult sub-model are the inputs for this sub-model (Figure 6). The main regulators of survival are physical removals and *in situ* mortality. The main modifiers are spawn location, egg density, incubation period, egg depth distribution, physical removal by waves and air exposure. Although carried over from the adult stage, embryo lipid reserves is a modifier primarily for the next stage (larval sub-model). There are many interactions among modifiers.

Much is known about the embryonic stage. Herring eggs are laid in multiple layers on kelp and rocks with 90% deposited between -5 and +2 m mean lower low water in PWS (Biggs and Baker 1993; Haegele et al. 1981). As in BC (Hay and McCarter 1997), spawning habitat does not appear limiting because PWS herring use a very small portion of the available shoreline. Incubation period is determined by air- and SST-

temperature and occurs over about 24 d in PWS (Biggs and Baker 1993) compared to 14 d in BC (Hourston and Haegele 1980) and is further modified by egg depth distribution and the timing of spawning (Haegele et al. 1981; Figure 6). In PWS, hatching peaks in early to mid-May (McGurk and Brown, 1996; Brown et al. 1996a; Rooper et al. 1996). Spawn location and egg depth distribution affect the orientation of eggs to wave energy and overlap with predators (e.g. shorebird flyways). Removals for Pacific herring, due to wave action and predation, can exceed 90% (Palsson 1984; Haegele and Schweigert 1991; McGurk 1991; Haegele 1993; Rooper et al. 1996) and are density dependent (Bishop and Green 2001; Rooper et al. 1996). A simple model of daily egg removal, based on cumulative time of air exposure, provided a good fit for measured removals in PWS (Rooper et al. 1996) and could be applied in the sub-model. *In situ* mortality, of eggs not removed, is also high and has also been modeled (Palsson 1984; Hay 1985; McGurk 1991; Biggs and Baker 1993). Desiccation, asphyxia, fungal infections, and plant toxins from red kelps (a common group in PWS) cause mortality to attached eggs (Rajasilta, et al. 1989).

Many eggs surviving incubation do not hatch or are not viable upon hatch. Egg density, incubation period, egg depth distribution, air and SST, and pollution all modify hatch and abnormalities. Hatching success is inversely proportional to herring egg density ranging from a mean survival rate of 0.16 at extremely high egg densities to 0.85 at low densities (Taylor 1971; Hourston et al. 1984; Johannessen 1986; McGurk 1991; Kocan et al. 1996a). Morphological deformities can affect 4-68% of the hatched larvae in natural conditions (Hourston et al. 1984; Purcell et al. 1990). Pollution can raise abnormality

rates even higher and stimulate premature hatch yielding smaller larvae (Kocan et al. 1996a). In PWS at 1989 EVOS exposed beaches, morphological abnormality rates rose to over 80% from a baseline of 55% while genetic abnormalities rose to over 40% doubling baseline rates of 10-22% (Kocan et al. 1996a; Hose et al. 1996). Genetically deformed or undersized larvae may become free-drifting larvae, but survival is tenuous (Hose and Brown 1998). An independent model of egg-larval survival in PWS, based on a relationship between egg and larval density, produced an overall baseline rate of 10-19%, with 0.5-0.7% from oiled beaches (McGurk and Brown 1996). A second deterministic model of viable larval production, based on combining stage-specific survival rates (McGurk 1991), produces a survival rate estimate of 1-4% for PWS. Either model can be incorporated in the embryo sub-model (Figure 6).

The larval stage is heavily influenced by conditions during the adult and embryonic stages. The modifiers that carry forward to the larval sub-model are lipid reserves, size-at-hatch, and hatch timing from the embryo sub-model (Figure 6) and spawn location and egg density from the adult sub-model (Figure 7). The main effects of size-at-hatch and hatch timing variability is the release of larvae in multiple batches, termed larval cohorts, resulting in a polymodal length frequency distribution for the year class (Lambert 1984; McGurk 1989). The impacts of this are discussed in the next section.

In summary, processes affecting embryonic survival are generally well documented and simple models have been developed that fit with observations. New research should focus on impacts of processes occurring during incubation on larval stage

dynamics. Existing models of egg-larval survival do not address impacts of larval size or hatch cohort patchiness on predation or removal rates. Experimental studies are needed to expand existing models to simulate conditions that formally could be compared with trends in recruitment.

The hypotheses generated in relation to year-class formation is:

H_n9. Year-class strength of the cohort is a direct and positive function of egg-larval survival (generated from a model).

Alternative H9. There is no correlation between egg survival and year-class strength. Rather, the cumulative effect of adult size-at-age, adult behavioral choices during reproduction, and environmental conditions during incubation will be correlated to year-class strength.

The process-oriented hypotheses generated from the embryo sub-model are:

H_n10 Egg removal through predation and wave-induced loss is the major regulator of egg survival to hatch followed by *in situ* mortality.

Alternative H10. None proposed since this hypothesis has been accepted, modeled, and well-documented (McGurk 1991; Rooper et al. 1996).

Corollary H10.1 Removals are density dependent and influenced by orientation to waves and air exposure, the egg depth distribution, and the incubation period.

Corollary H10.2. *In situ* mortality is density dependent and influenced by orientation to air and water circulation, meteorological conditions during incubation, the incubation period and pollution.

H_n11. Post-hatch survival to free-swimming yolk-sac larvae is a function of percentage hatch, abnormality rates, and predation.

Corollary $H_n11.1$. Percentage hatch and abnormality rates are density-dependent and a function of the incubation period and conditions during incubation.

Corollary $H_n11.2$. Pollution can significantly modify abnormality rates, predation rates, and hatch timing

Alternative H11. None proposed since these processes have been documented (Hourston et al. 1984; Johannessen 1986; Purcell at al. 1990; McGurk 1991; Kocan et al. 1996a).

H_n12 Lipid reserves and size-at-hatch are a function of embryo lipid reserves, egg density, the incubation period, conditions during incubation, and pollution.

Corollary H12.1. The incubation period is a function of conditions during incubation.

Alternative H12. None proposed since these processes are well documented (Haegele et al. 1981; Hourston et al. 1984; Lambert 1984; McGurk 1991; Kocan et al. 1996a).

H_n13. Egg depth distribution is random.

Alternative H13. The egg depth distribution is a function of egg density and spawn location.

Corollary H13.1. Hatch timing is a function of the egg depth distribution, conditions during incubation, the incubation period and pollution.

The Larval Sub-Model

The input to this model is the number and size-distribution of free-swimming larvae with key modifiers, especially location at hatch, passed on from previous stages (Figure 7). The adaptive spawn timing and location of the adults (Winters and Wheeler 1996) is compensatory with larvae hatching during a period of minimal upwelling and maximum retention in favorable rearing areas (Cushing 1975; Lasker 1985; Sinclair 1988). Therefore, spawning beaches can be viewed as "launch pads" for the larval stage with characteristics of a given spawning location (e.g. kelp type, substrate, risk to egg loss) of secondary importance to hatch location. The location, numbers, and sizes of larval batches determine spatial patchiness that influences overlap with food and encounter rates with predators (McGurk 1986). Herring larvae are known to remain aggregated (Henri, et al. 1985; Sinclair and Iles 1985; McGurk 1989; McGurk et al. 1993; Gallego and Heath, 1994b). This temporal segregation of larval release is probably an adaptive strategy to minimize probabilities of encounter with competitors or predators (Lambert 1984; McGurk 1984) and results in the stabilization of overall loss rates to the population.

At the early larval stage, the main regulators are predation, advection, and starvation. Growth, condition, pollution, and the abnormality rate are the modifiers that interact with one another and directly affect the regulation of survival. Larval mortality is stage-specific and probably highest at the early larval stage (McGurk 1993). Overall, observed mortality rates of Pacific herring larvae from BC, Alaska and Japan range from 0.0020 to 0.4039 d^{-1} with Alaska rates being intermediate (McGurk 1993). Early larval

mortality rates in the Bering Sea herring averaged of 0.1508 d^{-1} from age 3-12 d and dropped substantially to 0.0005 d^{-1} from age 13-63 d (Wespestad 1991).

Generally, food is not considered limiting in Alaska. Larvae must intersect food resources by about day 9 with 4-6 days of yolk-sac reserves (McGurk 1984). Herring larvae are relatively resistant to starvation in all but the most severe conditions (Kiørbe and Munk 1986) and starvation is not known to be a significant factor in Alaska (McGurk et al., 1990; Wespestad 1991; McGurk, et al. 1993). Alaskan herring larvae feed mainly on copepod eggs, nauplii, and copepodites (Wespestad 1991; McGurk et al. 1993) and later on *Pseudocalanus* spp., upper stage copepodites, and euphasids (McGurk et al. 1990). Jellyfish compete for food with herring larvae and may negatively affect Pacific herring larval growth rates in years of high jellfyfish abundant (Purcell 1990; Purcell and Sturdevant 2001). On the East Coast, zooplankton and growth were found to be the most important determinants in larval survival (Campbell and Graham, 1991) and food limitations were observed (Werner and Blaxter 1980, 1981). From Alaskan studies, growth is not density-dependent, observed growth differences are between patches with different hatch timing, and prey density is not a limiting factor toward larval growth (McGurk et al. 1990; McGurk et. al. 1993; Wespestad 1991). The initial conditions from the embryo stage, resulting in small post-hatch larvae or late spawn timing, are more influential on depressed growth than either larval or prey densities (McGurk et al. 1993).

Predation can be severe during the early larval stage. Reactivity is limited in clupeoid larvae until retinal development occurs (Higgs and Fuiman 1998) increasing early larval susceptibility to predation. However, there seems to be no relationship

between size, age (in days), and predation risk (Bertram and Leggett 1994). The only predator avoidance mechanism herring larvae possess is lack of pigmentation (Blaxter et al. 1982). Predation losses by jellyfish and ctenophores probably exceed those from any other predator species, ranging from mean instantaneous rates from 0 to over 90% d^{-1} (Stevenson 1962; Arai and Hay 1982; Purcell et al. 1990; Purcell and Grover, 1990) with most below 12.5% d^{-1} (Purcell et al. 1990). Although piscivory (Brodeur et al. 1987) and cannibalism (Hourston et al. 1981a; Wespestad 1991) of Pacific herring larvae have been observed, they have never been found to be considered significant in the diets of the fish examined (Paul 1982; Jewett and Blanchard 1997; Foy and Norcross 1999; Sturdevant 1999).

Predation may elevate mortality at metamorphosis. As herring develop schooling behavior, aggregate, and increase pigmentation, they are more visible and vulnerable to predation (Gallego and Heath, 1994a). Predation rates on pre-metamorphic larvae are about double that for post-metamorphic juveniles.

Pollution, such as oil spills, can be an episodic or chronic modifier of herring larval mortality. Larvae exposed to oil had lesions, pericardial edema, and genotoxic damage (Marty et al. 1997). They were shorter, had less ingested food, showed slower growth than larvae from unexposed sites. In PWS, the combination of exposure to oil during the egg stage and continued exposure of at least a portion of the drifting larval stage, resulted in higher rates of abnormalities (Norcross et al. 1996), mortality (McGurk 1990), and the lowest larval growth rate ever reported for Pacific herring (Norcross et al.

1996). Thus, exposure to oil can explain a failed year class such as the 1989 year class in PWS (Brown, et al. 1996b).

Advection may be the other main regulator of larval survival with initial distribution a key modifier. However, retention, versus advection, has been more commonly observed in most North Pacific locations and vertical migration behavior does not appear to control retention. Pacific herring are susceptible to wind-driven, tidal and residual surface currents as they are generally concentrated in the upper 2 m in early stages to 10 m as they approach metamorphosis (Stevenson 1962). In PWS, 98% of the herring larvae were captured in the upper 25 m (Norcross and Frandsen 1996) and may be restricted there due to the low tolerance (< 1 ° C change) for temperature gradients (Thornton 2003). Herring larvae perform diel vertical migration (Stevenson 1962; Henri et al. 1985; Munk et al. 1989) and vertical migrations are stimulated by food and light, rather than predation or positioning for transport (Henri et al. 1985; Munk and Kiorboe 1985). Although density of preferred food peaks at the pycnocline, larvae migrate according to a compromise between optimal light and prey densities that will maximize growth (Munk et al.1989). Their reaction to differentials in food density is to change swimming speed (Munk et al. 1989). Vertical migration and physical transport appear to be independent processes (Lazzari et al. 1993). On the East Coast, transport and temperature are considered secondary factors to food and growth for larval survival (Campbell and Graham 1991). Most larvae in BC are found in inside waters and therefore the importance of advection to larval mortality is questionable (Hay and McCarter 1997). Spawn locations, rather than vertical migration, resulted in retention on the west coast of

BC, and offshore dispersal rates reported were the lowest ever reported for herring (McGurk 1989). In Southeast Alaska (SE AK), spawning locations resulted in retention of larvae mainly within inner portions of Sitka Sound (Haldorson and Collie 1991). In the eastern Bering Sea, the shallow exposed shelf is very different environment from the coastal fjords, bays and passes in BC, SE AK, and PWS. There, spawning grounds are oriented to allow wind-driven retention of larvae (Wespestad 1991). Wind-driven larval transport is one of three factors explaining about one half of the variability in year-class strength of Pacific herring. Therefore, larval advection may contribute more to larval mortality in spawning areas adjacent to open ocean than areas inside fjords and inlets where local circulation enhances retention.

Larval retention within and advection out of PWS have been demonstrated with field measurements in 1989 (Norcross and Frandsen 1996). In 1989, spawn was evenly distributed among the NE, MT, NI and NS (Figure 1) and the population was near the maximum level over a 20 yr period (Brown et al. 1996b). Despite the large relative amount of spawn in the northeast and north, a large portion of the larvae was captured in the western and southwestern portions (Norcross and Frandsen 1996). Therefore, advection is a potential source of larval mortality in PWS.

Larval transport also has been modeled in PWS. A model was fit for transport from two northern (NE and NS, Figure 1), one central (NI) and one southern (MT) site in PWS using 1989 field data to identify and validate the best-fit model (McGurk et al. 1990). The best model (r^2=0.88; p <= 0.003) incorporated time-dependent turbulent diffusion, horizontal variance that increased exponentially with time, and non-constant

mortality. Diffusion rates were significantly different among sites. Advection from northern sites was less than from southern sites. Larvae from Montague Island (MT; Figure 1), closest to the entrance and exit flow of PWS waters, had the greatest dispersion rate with transport mainly northward from the inward flow from the GOA. Transport from the south and retention in the north should ultimately result in concentration of juvenile herring in northern PWS (McGurk et al. 1990).

A second PWS transport model used an ocean circulation model (Wang et al. 1997; 2001) to simulate drift of larvae from a known distribution of 1996 spawn in four regions (Norcross et al. 2001). Larvae were "released" during their normal hatch period in May and were tracked in the model until September (Figure 8). Model output was summarized mid-month from May until August (Tables 1 and 2). Data were tabulated by each of the four "release" or spawn regions and summarized by four destination regions: eastern, northern, southwestern, and the central gyre (Figure 9). In all destination regions except southwestern PWS, at least 80% of larvae were in place by May 16 (Table 1) indicating that drift to destinations occurred relatively fast. In southwestern PWS, only 20% of the larvae were in place by May, with 58% coming in by June, and 20% by July. From the simulation, a gradient of retention was evident with the highest in eastern and northern spawn regions (99.9% from southeast spawn, 40.2% from northeastern spawn, and 53.8% from northern spawn; Table 1). The lowest retention occurred from southwestern spawn (4.9%). This retention pattern and the numbers of larvae released from each spawn area dictated the ultimate contribution by spawn area to the destination regions. For example, despite poor retention of larvae within the southwestern region, the

southwestern spawn region (MT, Table 2) contributed over 50% of the larvae to three regions because most larvae (54.1%; Table 1) originated there. The most interesting outcome was accumulation of larvae (53.3% of all larvae released; Table 1) in the center of PWS within the central gyre most of which came from southwestern spawn (MT, 69.5%; Table 2). This central gyre may ultimately act as a "trap" for larvae (Figure 9) and represent advection mortality since larvae are transported away from favorable nearshore rearing areas. Although the model was not validated with larval catches, the northern drift pattern from southwest (MT) spawn and northern retention is in concurrence with results from McGurk's model (McGurk et al. 1990) providing some substantiation of the drift simulation.

In PWS, metamorphic herring entered an array of broadly distributed nursery habitats by mid-July, after spending about 60 days at sea, and were 35 mm in length (Figure 10; Stokesbury et. al. 1999b). This is very similar to the size and duration at metamorphosis of BC Pacific (Stocker 1993) and Atlantic herring (Gallego and Heath 1994a).

Modeling the larval stage may be a critical step to gaining a better understanding of recruitment variability if larval mortality rates are deterministic of year-class strength. In a sensitivity analysis performed on Atlantic herring, recruitment was controlled by density-dependent predation on juveniles only in years of high larval survival; otherwise recruitment was dictated by survival of the larval stage (Campbell and Graham, 1991). The range of larval survival rates is the lowest of all the stage-specific survival rates reviewed for Pacific herring (Norcross and Brown 2001).

In summary, spatially explicit models at the larval stage have been developed but improvements are needed to incorporate processes due to behavior, exposure to pollutants, and bioenergetics. The larval drift simulation models underscore the importance of spawn location to larval retention and advection, but the models generally lack appropriate validation. Adding a behavioral bioenergetic component, that predicts vertical movement (e.g. Clark and Levy 1988), would improve the models. Adding realistic boundary conditions, such as the mixed layer and vertical temperature profile should be used as boundary conditions. Using a combination of modeled larval condition, hatch location, and the drift simulation, tests of effects on recruitment are possible.

The hypothesis generated relating to year-class formation is:

H_n14. In most years, model output and applied mortality rates are correlated to year-class strength because larval mortality is relatively constant and low. Strong year-class outliers represent exceptional larval survival, while weak year-class outliers represent anomalous event-driven conditions (e.g. large jellyfish bloom, high wind years with non-optimal mixing and turbulence, oil spills).

The process-oriented hypotheses generated from the larval sub-model are:

H_n15. Early larval survival is relatively constant and any variations observed are random.

Corollary $H_n15.1$. Predation is constant or a random process.

Corollary $H_n15.2$. Pollution has no effect on rates of predation on larvae.

Corollary $H_n15.3$. Advection is a chaotic process with no predictable patterns.

Alternative H15. Early larval survival (first 10 d) is regulated by predation removals, advection away from nursery habitats, and starvation; the apportionment of effect is region-specific.

Corollary H15.1. Predation is a function of size at hatch, spatial patchiness of larvae dictating overlap with predators, and predator species composition and abundance.

Corollary H15.2. Spatial patchiness is a function of the location and extent of spawn, egg density, and numbers of larval cohorts dictated by hatch timing.

Corollary H15.3. Pollution can directly or indirectly alter larval size and abnormalities, predation rates.

Corollary H15.4. Advection is a function of larval size, temporal overlap with favorable conditions, and "launch" site determined by spawn location.

Corollary H15.5. Overlap with favorable conditions is dictated by hatch timing, spawn location, hydrographic conditions including availability of larval food, mixed layer depth and duration, upwelling, sea surface currents, and wind events.

Corollary H15.6. Starvation is a function of lipid reserves at hatch, size at hatch, and overlap with favorable conditions.

H_n16. Later larval survival is relatively constant or variations in survival are random.

Corollary H_n16.1. Predation is constant or a random process.

Corollary H_n16.2. Advection is a chaotic process with no predictable patterns.

Alternative H16. Late-stage (> 10 d old) larval survival is regulated by predation and advection; the apportionment of effect is region-specific.

Corollary H16.1. Predation is a function of spatial overlap with predators, larval stage duration, larval growth, condition and size at metamorphosis and location at metamorphosis.

Corollary H16.2. Advection is a function of larval stage duration and temporal overlap with favorable conditions.

The Juvenile Sub-Model

As predicted by the larval transport model, PWS juvenile herring exhibit a broad, nearshore distribution in PWS and the OK (Figure 1; Figure 10; Stokesbury et al. 1999a; Norcross et al. 2001) similar to the nursery habitat described for BC (Hourston 1956, 1957, 1959; Haegele 1995). Although PWS adult herring are found in many of the same areas as juveniles, they are probably seasonal migrants and do not school with juvenile herring (Stokesbury et al. 1999a). Therefore, interactions with adults are probably not needed in the juvenile sub-model (Figure 11). In July, metamorphic larvae were found at the mouths while age-1 herring were generally at the head of bays; by fall, both ages were found throughout the bays (Stokesbury et al. 1999a). Nursery habitats in PWS are generally bays that are weakly to strongly stratified in summer with abundant zooplankton and well mixed in spring and winter (Norcross et al. 2001). PWS juvenile herring spend two winters in the nurseries (Stokesbury et al. 1999a) compared to one or two in BC (Haegele 1995; Hay and McCarter 1997).

Similar to other juvenile fishes, herring precariously balance between feeding and being eaten (Walters and Juanes, 1993). Juvenile herring must remain in the illuminated surface waters to feed on the zooplankton. As day length grows in the spring, herring are visually exposed to predators for longer periods making them increasingly vulnerable to seabirds from above and piscivorous fish from below. In PWS, juveniles were never found deeper than 30 m (in March) with the majority 17 m or less by July (Stokesbury et al. 1999a). During daylight, schooling behavior becomes the main defense against predation. In PWS, tightly schooled age-1 herring at the surface are first observed in late April in a given year (Brown et al.1999) when the zooplankton bloom is well underway (Cooney et al. 2001).

Modifiers from the larval sub-model (Figure 7) carried into the juvenile sub-model (Figure 11) are the location, condition, and size at metamorphosis (Figure 11). Because density-dependent processes may be important, the number and density of new arrivals at nursery areas can be considered a modifier as is the abundance and size structure of the previous cohort already occupying the bay (Figure 11).

The major regulators of juvenile survival are probably predation and disease. In this model, predation and disease may be density-dependent and modified by juvenile growth and condition (based on Walters and Juanes 1993), the size and species composition of predator and competitor populations (Fernö et al. 1998), the abundance and energy density of zooplankton as herring prey (based on Foy and Norcross 1999) and as alternative prey for herring predators (Fernö et al. 1998), and pollution (Carls et al.

1998). The modifiers may interact in a complex, highly variable manner and this complexity has been represented as a single modifier called "habitat quality" (Figure 11).

There are few estimates of young-of-the-year (YOY) herring mortality in the literature. The average instantaneous natural mortality (*M*) for PWS YOY is 0.009 (SD = 0.002; 1996 cohort) and 0.016 (SD = 0.012; 1997) and for age-1 herring, 0.003 (SD = 0.007; 1995) and 0.008 (SD = 0.005; 1996) (Stokesbury et al. 2002). These rates are comparable to a single estimate for Norwegian herring of 0.0077 d^{-1} for 16 g YOY Atlantic herring (Dragesund 1970) but far lower than one for BC herring during the fall at.0.12 d^{-1} (Taylor 1964). Using an energetic model with individual lipid content and temperature as main inputs over a 135 d period, overwinter survival was estimated in four bays over a 3-yr period to range from 5-95% with considerable variability among bays and years (Norcross et al. 2001). Some bays showed consistently higher survival rates among years than others. Although it is not clear whether available rearing habitat is limiting to PWS juvenile herring, these results indicate that certain nurseries may be better than others.

Predation

Predation pressure is high on juvenile herring and varies by predator species. Piscivory may be the primary source of predation mortality. Pacific cod (*Gadus macrocephalus*) in BC individually consumed several hundred age-0 and –1 herring resulting in a cod-specific predation rate (*M*) of 0.75 yr^{-1} (Walters et al. 1986). In PWS, juvenile herring are observed in the stomachs of locally abundant juvenile and adult pollock (*Theragra chalcogramma*), other cod species, halibut (*Hippoglossus elassodon*),

arrowtooth flounder (*Artheresthes stomias*), greenlings (*Hexagrammos* sps.) and being fed upon by squid (species unknown) (Stokesbury et al. 2002). Heavy predation on PWS Age-0 occurs by multiple species of seabirds (Irons 1992; Duffy 2000). Some seabirds such as puffins or marbled murrelets select for smaller fish (Furness and Furness 1985) like age-0 herring in PWS, (Hatch and Sanger 1992). PWS kittiwakes show a preference for age-1 herring and will feed on age-0 or other forage fish only in the absence of this age class (Suryan et al. 2000). This author observed humpback whales passing over numerous schools of age-0 herring to feed on larger, older herring. Predation dynamics are therefore specific to predator species or class of predator.

Given the current extremely low population level, it is possible that PWS herring are in a "predator pit" (Hilborn and Mangel, 1997). Generally there may be smaller schools along with fewer aggregations over a smaller geographic range. If juvenile herring spend more time at the edge of schools, a high predation risk position, and the overall affect is stabilization of the population at low levels (Walters and Juanes 1993). Despite an increase in aggregations and geographic range, if schools remain small, predation may continue to be high. Changes in ocean conditions and spawning dynamics that alter larval dispersions patterns may result in larger schools and a drop in predation. The overall result is non-stationarity in stock-recruitment patterns (Walters and Juanes 1993). Similarly for adult herring, a small number of small schools combined with stable or increasing predator population in PWS could act to maintain or reduce the population level.

Growth and Condition

Summer growth rates in age-0 herring (Stokesbury et al. 1999b) and condition, in terms of whole body energy content (WBEC; Paul and Paul 1999) are highly variable among nursery areas in PWS reflecting the spatial variability in environmental conditions and habitat quality (Foy and Norcross 1999). During the winter, when growth rates are generally depressed, differences in rates among bays disappear (Stokesbury et al. 1999b). There is a high degree of inter-annual variability in growth and the within-year spatial differences between nursery sites are not consistent between years. Unlike the estimated mortality rates, no one site exhibits consistently higher growth than any other site (Stokesbury et al. 1999b). During winter, PWS age-0 herring cannot maintain their metabolic needs from feeding and rely on energy stores gained in summer and fall to survive (Foy and Paul 1999). Although zooplankton biomass is not significantly different among bays and years (Norcross et al. 2001), energy density of prey is different (Foy and Norcross 1999). However, the pattern of observed diet energy does not match the pattern of WBEC, but WBEC and growth are similar (see Norcross et al. 2001) indicating a link between condition and growth. The mismatch in observed prey energy density and WBEC might be caused by intra-species competition. In the PWS study, the site with the smallest and lowest WBEC herring also had high densities of age-0 herring (Norcross et al. 2001). The WBEC and prey energy density results underscore the potential importance of competition in the model. The variability in growth and WBEC underscore the importance of patch size and reactive scale to environmental variability in modeling the juvenile stage.

Density-dependent processes and competition are modifiers of habitat quality in the juvenile sub-model (Figure 11). Juvenile herring are able to "crop down" their food supply in dense schools (Arrhenius 1997). Within a nursery bay, grazing competition is cited as a potential cause of low zooplankton biomass and is evidenced by observed small individual fish size (Norcross et al. 2001). Juvenile herring compete with jellyfish and other small fish as a large amount of dietary overlap is found among species in herring nursery areas (Purcell and Sturdevant 2001). Diets and feeding rates of juvenile sand lance, pink salmon, and herring change in the presence of one another (Purcell and Sturdevant 2001). In allopatric distributions, diets of sand lance and herring are similar and pink salmon are different. In sympatric distributions, diets of sand lance shifted and feeding rates are reduced in all three species. Zooplankton densities in the water column are higher in allopatric than in sympatric distributions (Purcell and Sturdevant 2001). Diets of juvenile herring and pollock are similar in summer and fall (Sturdevant 1999). In areas of co-ocurrence, pollock and herring vertically apportion the habitat by occurring at different depths (Stokesbury et al. 1999a; Sturdevant 1999) possibly to avoid competing. However, the risk of competition between pollock and herring is especially acute during the fall when zooplankton biomass is low but diet overlap is high (Sturdevant 1999; Purcell and Sturdevant 2001).

Disease and pollution can further modify the effects of density-dependent processes and competition. Young herring have not developed immunity and thus are extremely susceptible to VHSV (the disease first observed in PWS in 1993); crowding induces epizootics (Kocan et al. 1995). Pollution affects density-dependent processes and

disease immunity. Juvenile Pacific herring exposed to oil show "classic stress response" including physiological signs and reduced swimming performance (Kennedy 1997). Despite physiological compensation occurs after a few days of continuous exposure, higher exposure levels result in increased stress-induced mortality.

Growth and Predation

For juvenile herring, it appears that growth, predation, and patch density are strongly linked in determining mortality rates. Size-dependent predation is cited as the main source of mortality in post-metamorphic age-0 herring (Blaxter 1985). Growth rates peak in the summer when food is abundant and zero or negative growth rates were observed in winter (Paul and Paul 1998; Stokesbury et al. 1999b). Negative growth rates indicated size-selective mortality in PWS, especially true in age-0 herring (Foy and Paul 1999; Stokesbury et al. 1999b). In years of low zooplankton abundance, larger fish may switch to feeding on small fish (Willette 2001; Willette et al. 2001) and increase size-dependent predation rates on juvenile herring over levels observed in years of moderate to high zooplankton productivity. Size-dependent predation may be due to the increased susceptibility of smaller fish. To gain storage energy needed to survive times of fast (Foy and Paul 1999), small fish must spend more time feeding than larger individuals, resulting in extended time spent in a predation window coupled with lowered avoidance capability in weaker individuals. However, size-dependent losses may be reduced in a given juvenile herring patch if growth is equalized through habitat selection processes (Hugie and Dill 1994). If larger individuals spend less time feeding and more time avoiding predators than smaller individuals, growth will be equalized (Walters and

Juanes, 1993). In this case, density-dependent mortality would not appear to be related to growth or food availability and year-class strength may be unrelated to size-at-age. Selection pressure should result in an optimum balance of growth and predation risk. This is modeled as foraging time proportional to a threshold size (size below which probability of survival to reproduction is zero) plus an additional time inversely proportional to the predation risk per time (Walters and Juanes 1993). In a different model, designed for a schooling planktivore, the ratio of food abundance to visual predation risk was most deterministic of growth and survival (Rosland 1997). These dynamic optimization or state models are probably most appropriate for the juvenile sub-model.

Population Membership

The juvenile sub-model ends with exit from nursery areas and the joining of age-2.5 immature herring with adult schools. Assuming that adult herring in a given area are members of a distinct local population, membership of the new recruits is determined by the membership of the adult schools intersected (e.g. Figure 4). This process of "joining" is poorly understood for herring and may be a key determinant of recruiting class size in a given population. The importance of this process to maintenance of a population is explained in a later section on metapopulations. Timing of joining may vary by region. Atlantic herring, juveniles join the adult populations from their respective nursery areas after the spring or fall spawning event (McQuinn 1997) while Pacific herring in BC join sometime before September or October in BC (Hay and McCarter 1997). Similar to BC, PWS age-2.5 herring leave the nursery in late summer (Stokesbury et al.1999b). Given the lack of observations, simulation modeling of herring movements may be important to

further understanding the joining process. A model of Atlantic herring locomotion was used to predict the movements of immature, age-2 herring during the summer in the Bay of Fundy (Jovellanos and Gaskin, 1983). The model assumed a herring-appropriate swim speed, positive rheotaxis, and crosscurrent movement frequency that varied inversely with the speed of the current. The model correctly predicted movements and was validated with observed locations from catches, acoustics, and foraging seabird flock locations. The model estimated size-segregation, residence time of migrating fish, and predicted detailed movements of schools with tidal flow. Output of similar models could be used to study spatially explicit contribution rates from nursery bays and mixing between nursery bays.

Summary and Hypotheses

In summary, the complex interaction of environmental variability and behavioral response of juvenile herring require more complex life-history models than are required for earlier life stages. Potentially appropriate models include habitat selection including size-dependent predation risk (Walters and Juanes 1993; Hugie and Dill 1994; Kitchell at el. 1994; Rosland 1997; Ryer and Olla 1998) or behavioral responses to competition with other species or older, larger fish of the same species (Crowder and Magnuson 1983). Juvenile herring perform diel migrations and models including that element may also be useful (e.g. Clark and Levy 1988). Coupled larval-juvenile models could simulate the additive effects from sequential life history stages (modifiers carried over between sub-models). Selection models with predation risk could be used to model the existence and severity of a "predator pit". Larval drift simulation models could provide initial

distributions of juveniles while movement models (Jovellanos and Gaskin, 1983) could be used to test stock structure theory. As with the larval models, the lack of validation data is a problem.

The hypothesis generated relating to year-class formation is:

H_n17. Vital rates and condition of juvenile herring are correlated with year-class strength.

Alternative H17. Only exceptionally strong year-classes are correlated with vital rates and condition of juvenile herring; environmental factors forcing juvenile herring will account for strong year-class outliers in models of recruitment.

Corollary H17.1 The summer abundance of age-1 herring is directly correlated with year-class strength two and three yrs later as most of the variability in year-class formation occurs prior to the cohort year or during age-0.

Corollary H17.2. Environmental conditions favorable to growth from age-1 to -3 and condition of age-1 herring determine the proportion of age-3 herring reaching sexual maturity and participating in the spawning event.

Corollary H17.3 Model residuals of the function between age-1 herring abundance and year-class strength two and three yrs later are correlated to predation or predator abundance.

The process-oriented hypotheses generated from the juvenile sub-model are:

H_n18. Survival of juveniles is not density- or size-dependent.

Corollary $H_n18.1$. There is no detectable effect of disease on juvenile herring removal rates by predation.

Corollary H_n18.2. Pollution has no effect on removal rates of juvenile herring.

Corollary H_n18.3. Predation rates are not spatially variable and depend only on juvenile herring density and size.

Corollary H_n18.4. Predation rates on juvenile herring are not dependent on low population levels, small numbers of aggregations, or small school sizes.

Alternative H18. Density- and size-dependent predation determines survival of juvenile herring.

Corollary H18.1. Condition-dependent disease occurrences increase the removal rate of juvenile herring by predation over that predicted by density- and size-dependency alone.

Corollary H18.2. Pollution increases predation rates via depressed juvenile herring growth rates

Corollary H18.3. Pollution decreases predation rates via removals of juvenile herring predators.

Corollary H18.4. Pollution induces disease over the level predicted by condition dependence alone.

Corollary H18.5. Predation rates are site-specific and vary according to predator population levels and species composition.

Corollary H18.6. Year-class formation may be restricted by the presence of a "predator pit" caused by small schools sizes or small numbers of aggregations over the geographic range of nursery sites and precipitated by low population levels.

H_n19. Growth and condition is not site-specific and is strictly a function of size and condition at metamorphosis.

Corollary $H_n19.1$. Nursery habitat quality is not significantly variable in a given population range of juvenile herring.

Alternative H19. Growth and condition of juvenile herring is dependent on the condition and size at metamorphosis and site-specific factors including the density of herring, nursery habitat quality and location, and pollution levels.

Corollary H19.1. Nursery habitat quality and location is dependent on zooplankton availability, competitor population levels, predator population levels, hydrographic conditions, and location at metamorphosis.

H_n20. Recruitment of age-2 herring to a given population is a random process and is independent of distribution or population size.

Alternative H20. Recruitment level of age-2 herring to a given population is dependent on the intersection rate with adult herring from that population.

Corollary H20.1. The probability of intersection of age-2 herring with adults is dependent on nursery habitat location, the size-dependent timing of exit from nursery areas, location of nursery areas, adult population level and adult distribution.

The Metapopulation Concept and Application to PWS

The biocomplexity of spatial stock structure and plasticity in herring reproductive characteristics may be an adaptive response (Thompson 1991). In effect, herring "cover all the bases" of environmental conditions encountered to increase the probability that in

some areas of occupation, conditions are optimal. The contraction of herring stocks in the Norwegian Sea after the 1960s stock collapse indicated a connection between stock size and distribution (Fernö et al. 1998). For Pacific herring, potential population size is restricted by the area of the adjacent continental shelf available; wide shelves have higher carrying capacities than narrow shelves (Hay and McCarter 1997). Although the quality of life stage-specific habitats between areas add variability to the relationship between stock size and shelf area, carrying capacity or a "trophic limitation" appears to occur at about 10g m^{-2} (Hay and McCarter 1997). Adding to spatial complexity, Pacific herring populations apparently occur in two basic stock structures within shelf areas (Stocker 1993; Hay et al. 1999); large migratory stocks range over large geographic regions (e.g. 10,000 km^2) and small non-migratory stocks range over smaller geographic areas (e.g. 500 km^2). Either stock strategy has risks. Herring possess a complex, multi-stage life history with very high early life mortality rates and a life-long center spot in the food chain. Maintenance of spatial biocomplexity along with a diversity of adaptive strategies could be critical for continuance of an abundant or healthy population. Sinclair (1988) refers to this concept as a "gradient of species richness" and underscores the importance of understanding spatial population structure to understand population trends. Bailey et al. (1998) demonstrated how spatial shifts in spawning distribution of North Sea Atlantic herring affected recruitment in opposition to spawner biomass trends. A clear understanding of a discrete population's life history processes in time and space must precede any interpretation of environmentally driven year class strength variation particular to that group.

Although there is agreement in the importance of spatial biocomplexity for maintenance of a population, there is disagreement about what constitutes a population. One view is that species consists of a number of dynamic and unstructured assemblages and biocomplexity in spawning areas is simply an expression of population expansion and contraction (Smith and Jamieson 1986). An opposing view divides species into a number of discrete unit populations with unique life histories in time and/or space and asserts that "vagrants" or individuals that emigrate represent losses (Iles and Sinclair, 1982; Sinclair, 1988). McQuinn (1997) proposed the "adopted-migrant hypothesis" as unification of two theoretical extremes in herring population theory based on the idea of metapopulations.

Metapopulations consist of an array of local populations linked by varying degrees of gene flow (Wade and McCauley 1988) with each locality surviving only if migrants balance vagrants (Levins 1968; McQuinn 1997). Levins (1968) first defined the metapopulation concept noting that the probability of local population extinction may depend on its genetic composition. Furthermore, migrants from within the metapopulation colonize vacant sites. Some local populations rely solely on retention and self-maintenance while others depend on vagrants and mixing for maintenance and therefore, genetic uniqueness may occur only at the metapopulation level. Metapopulation theory has gained considerable popularity in a number of ecological settings (Hastings and Harrison 1994). In the application to herring, McQuinn (1997) proposed that local population affinity is established at the time of first maturation and

fixed for all subsequent spawnings. He surmises that recruitment to local populations occurs when juveniles join adult groups during the out-migration from spawning events.

Maintenance of herring spatial biocomplexity and metapopulation structure probably occurs at the scale of individual school units or aggregations. Behavioral mechanisms at the school level maintain spacing between schools independent of stock size and probably result in the kinds of spawning expansions and contractions observed in the Norwegian Sea (Fernö et al. 1998). Fernö et al. (1998) suggest an adaptive mechanism whereby an aggregation of herring return to a formerly successful spawning area, but they are relatively plastic in spawn timing and exact beach location reacting to interannual variations in ocean conditions. New recruits that have joined the aggregation learn from the adults where to spawn, a process called "spatial learning" (McQuinn 1997). The fidelity of these aggregations to their respective spawning areas maintains the observed spatial structure of a given population (Hourston 1982). Therefore, the aggregation or "patch" of closely associated aggregations is probably the appropriate unit for analysis of herring spatial dynamics. Given population decline in a given region, more non-continuous spawning segments along a shoreline may occur reflecting fewer total aggregations spawning. In the absence of recruits to join existing aggregations, spawning in a given region may cease altogether through attrition.

The metapopulation framework is useful for conceptualizing a stock structure for PWS and the OK Peninsula (Figure 1). For the purpose of this paper, we define the PWS metapopulation as a collection of local populations. Each local population is a functionally operational spawning and recruitment unit within a spatially explicit

geographic region that may or may not require migrants to avoid extinction. Unique local population characteristics, such as growth and survival, result from unique regional forcing variables (physical or biological) that may or may not overlap with other units. Recruitment rates may vary among local populations according to the spatial structure with the region and degree of overlap between recruiting juveniles and adults. This definition is very similar to those proposed by McQuinn (1997) and Stephenson (1999).

The lack of genetic differentiation among local units is due to extensive early life history mixing. Historically, there was a lack of evidence supporting Pacific herring genetic uniqueness (Grant and Utter 1984; Burkey 1986) thought to be due to extensive mixing at the larval stage as in other marine fish species (Smith and Jamieson 1986). Weak genetic evidence of population sub-structure in PWS was provided by a recent study using microsatellite DNA, which is known to detect finer scale genetic differences compared to old methods. Genetic differences were found between eastern and southwestern regions of PWS, and between PWS and other Alaskan regions (O'Connell et al. 1998). Herring from Kodiak Island (Figure 1), located 300 km southwest and downstream via the Alaska Coastal Current (ACC) of PWS, were more similar to herring from southwestern PWS than eastern and southwestern PWS herring were to each other. This finding indicates the potential importance of PWS in providing vagrants to Kodiak populations due to larval "leakage" out of PWS. If the recent genetic study results are truly due to spatial segregation, than regional variation in herring population dynamics may represent the local populations comprising the greater PWS metapopulation. Additional microsatellite DNA research and analysis of other biological markers, such as

chemical composition of otoliths (Campana et al. 1994; Thresher 1999) and fatty acid composition, may be useful in identifying local populations.

Results from the larval transport models (Tables 1 and 2, Figure 8) indicate a potential regional split with the high retention eastern region (Figure 9), the low retention southwestern region, and the northern region with moderate retention. Because of the apparent reliance on vagrants from the eastern and northern regions, the overall abundance of herring in PWS may remain low if the PWS metapopulation is reduced to mainly spawning on Montague Island (MT; Figure 1). The current situation in PWS is a depressed population, due to the lack of a strong recruiting year class in recent years, and MT dominated spawning (Fritz Funk, Alaska Department of Fish and Game, personal communication). Because the northern region has both retention and migrants, the population there could theoretically maintain itself in the absence of Montague spawning. Larvae ending in the central gyre may represent advective losses in addition to those swept in the GOA. The gyre may be a "trap" leaving larvae near a high oceanic food supply (GOA copepods; Kline 1999) but facing metamorphosis in a highly exposed and risky environment; it is possible high mortality occurs there.

To contribute to a given local population, the larvae may need to metamorphose at suitable rearing habitats located where it is possible to intersect with the migratory path of PWS adults from that population (e.g. Figure 5). Given the high degree of variability in nursery habitat quality and juvenile herring survival in PWS (Norcross et al. 2001), the arrival location during metamorphosis may have a major impact year-class formation. If larvae arrive at good nursery habitat where juvenile survival rates are high, but in areas

where contribution rates back to the local population is low, the result may be low recruitment rates. Alternatively, if the larvae arrive at poor or highly variable quality habitat where survival rates are low or variable, but the contribution rates are high, the result may also be low or variable recruitment rates. In an ecosystem like PWS, a combination of outlined situations is probable. However, given the current low abundance of adult herring in all regions of PWS, the probability of intersection with adults may be low resulting in impaired "spatial learning" (McQuinn 1997) by potential recruits.

Metapopulation Hypothesis for PWS

I therefore hypothesize that the PWS metapopulation comprises two well defined (Eastern and Southwestern) and a third less defined (Northern) local population groupings (Figure 9). Furthermore, each possesses unique adaptive strategies for successful recruitment. The eastern and northern populations are non-migratory, have moderate to high retention characteristics and moderate to low vagrancy. Given at least some spawning, variability in recruitment to the eastern and northern populations should be mainly determined by environmental characteristics and a threshold level of resident adults to provide spatial learning. Migrants from the southwest add to the eastern and northern local populations, but are not required to produce a successful year-class. In contrast, the southwestern population is migratory, has low retention and high vagrancy. Variability in survival and year-class formation in the southwest is related to environmental characteristics at the PWS-GOA interface as well as larval drift and survival of migrant recruits from the east and north. Strong year classes can only be

formed in the southwest with a combination of favorable environmental conditions and eastern or northern migrants recruited in the larval stage.

An alternative hypothesis is that regional colonization and spatial complexity of adult spawning aggregations is solely a function of population size (e.g. Smith and Jamieson 1986). Spatial complexity increases with population size and shrinks with low populations along a gradient of habitat quality. For this alternative, recruitment is unrelated to spatial distribution of adults and intersection rates with juveniles exiting nursery bays. This hypothesis falls within the guidelines of the Basin Theory by MacCall (1990) in which habitat choice leads to equity in individual fitness and that the population will shrink to the highest quality habitat resulting in the highest realized fitness. As the population grows, habitat quality is affected by density and although individual fitness is equalized, overall habitat quality will be lower. Characteristics of the population under this theory might include genetic homogeneity, migration paths radiating outward from prime habitat in relation to population size, and low spatial variability in adult growth (or another measure of fitness) over the range of population distribution.

The ratio of recruit per spawner (R/S) may be an indicator of the appropriate population theory. If the alternative theory is correct and spatial complexity is simply a function of population size, the R/S relationship may conform to a well-defined model, especially with the inclusion of key environmental forcing factors on year-class formation. However, if metapopulation theory more appropriately represents the situation, the R/S relationship may be hard to define, even with inclusion of environmental factors, unless modeled by local population. Because both the spatial

pathways used during the life histories and the local environmental forcing differ among local populations, only the inclusion of both can result in a representative R/S model. Results in Chapter 2 show that R/S production is dependent on allocation to spawn areas (i.e. spatial complexity) rather than population level providing evidence for the PWS metapopulation theory.

Model Summary and Conclusion

The conceptual stock model presented here can be used to test population theory as it includes both spatial pathways and environmental forcing. A key idea proposed is in a given population, variability of life history parameters will be life-stage specific and depend on the number and spacing of patches, the within-patch density, the ratio of the reactive patch scale to the scale of environmental variability, and the magnitude of environmental forcing. The intention of this paper is not to quantify and computerize the model, but rather as a guideline for ordering information, developing testable hypotheses, and building population theory. However, many of the embryo and larval stage sub-model components (Figures 6 and 7) have been parameterized and simulations of these sub-models would require a small amount of additional effort. Many of the adult sub-model components are also well understood and only the initial state (numbers of incoming 2.5 yr recruits; Figure 5) is not generally known. The juvenile sub-model is the most complex with the greatest number of unknown parameters of all the sub-models yet it is required to feed the initial state of the adult sub-model and complete the life history loop. However, if the goal of model simulation is to test stock structure theory, the adult, embryo and larval sub-models could be simulated and a range of juvenile survival

assumed providing a spatially explicit range of R/S ratios. In this way, multiple year simulations would produce a range of curves that could be compared to actual R/S models derived from fishery stock assessment data. This effort would represent a unique approach to stock assessment modeling and include, in a meaningful way, environmental factors needed to adopt an ever-popular ecosystem approach.

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Table 1.1. Seasonal and total allocation of larvae to each destination region (Figure 9) from each of the four spawning areas in Prince William Sound (PWS; Figure 1), Alaska according to the larval drift simulation study (Norcross et al. 2001). The spawning regions are northern Montague Island (MT), the north shore (NS), southeastern (SE) and northeastern (NE). Percentages add to 100% vertically. Percentages of larvae transported from other regions are italicized and retained larvae (originated within the region) are not italicized.

Starting Values:		**MT**	**NS**	**SE**	**NE**	**All Areas Combined**		
Total Nos. Released		**1.46 E+12**	**7.30 E+10**	**2.19 E+11**	**9.49 E+11**	**2.70E+12**		
Percentage Released		**54.1%**	**2.7%**	**8.1%**	**35.1%**	**100%**	**% Allocation of Larvae to Destination Regions**	**% Monthly Contri-bution to Each Destination Region**
Destination Region:	**Date of Simulation**	**Allocation of Larvae Among Destination Regions from Each Spawn Area:**				**Total Nos. at Regions**		
Eastern	16-May	2.8E+08	0.0E+00	1.1E+10	2.8E+10	3.8E+10		88.4%
	16-Jun	2.6E+08	0.0E+00	1.5E+09	7.6E+08	2.5E+09		5.8%
	16-Jul	6.7E+08	2.9E+07	4.8E+08	8.6E+08	2.0E+09		4.8%
	16-Aug	1.5E+08	7.8E+06	1.1E+08	1.9E+08	4.6E+08		1.1%
	% *Transport* or Retention	***1.6%***	***1.0%***	**99.9%**	**40.2%**	**4.3E+10**	**23.9%**	**100%**
Northern	16-May	1.1E+10	1.8E+09	0.0E+00	1.1E+10	2.3E+10		79.7%
	16-Jun	3.3E+09	1.3E+08	0.0E+00	4.3E+08	3.8E+09		13.1%
	16-Jul	1.2E+09	4.9E+07	2.2E+06	5.6E+08	1.8E+09		6.2%
	16-Aug	2.0E+08	4.8E+06	3.4E+06	8.9E+07	3.0E+08		1.0%
	% *Transport* or Retention	***17.5%***	**53.8%**	***0.1%***	***16.4%***	**2.9E+10**	**16.1%**	**100%**
Southwestern	16-May	0.0E+00	1.5E+09	0.0E+00	2.4E+08	1.8E+09		20.4%
	16-Jun	3.1E+09	9.1E+07	0.0E+00	1.8E+09	5.0E+09		58.3%
	16-Jul	1.2E+09	7.3E+07	3.7E+05	4.5E+08	1.7E+09		19.5%
	16-Aug	1.2E+08	1.2E+07	1.7E+05	2.8E+07	1.6E+08		1.8%
	% *Transport* or Retention	**4.9%**	***45.2%***	***0.0%***	***3.5%***	**8.6E+09**	**4.8%**	**100%**
Central Gyre	16-May	6.3E+10	0.0E+00	0.0E+00	2.7E+10	9.1E+10		94.6%
	16-Jun	2.9E+09	0.0E+00	0.0E+00	7.6E+08	3.6E+09		3.8%
	16-Jul	3.9E+08	0.0E+00	0.0E+00	8.5E+08	1.2E+09		1.3%
	16-Aug	8.7E+07	0.0E+00	0.0E+00	1.9E+08	2.8E+08		0.3%
	% *Transport* or Retention	***76.0%***	***0.0%***	***0.0%***	***40.0%***	**9.6E+10**	**53.3%**	**100%**
							100%	
		100%	**100%**	**100%**	**100%**			
Grand Total (Add Nos Down)		**8.8E+10**	**3.7E+09**	**1.2E+10**	**7.3E+10**	**1.8E+11**		

Table 1.2. Percentage contribution of larvae by each of the four spawning regions (Figure 1) to the destination regions (Figure 9) in Prince William Sound, Alaska, according to the larval drift simulation study (Norcross et al. 2001). The spawning regions are northern Montague Island (MT), the north shore (NS), southeastern (SE) and northeastern (NE). Percentages add to 100% horizontally.

	% Contribution by Spawn Area to Destination				
Destination Region:	**MT**	**NS**	**SE**	**NE**	**Total**
% to Eastern	3.2%	0.1%	28.1%	68.6%	100%
% to Northern	52.3%	6.9%	0.02%	40.8%	100%
% to Southweastern	50.4%	19.7%	0.01%	29.9%	100%
% to Central Gyre	69.5%	0.0%	0.0%	30.5%	100%
% Grand Total to All Regions	**49.7%**	**2.1%**	**6.8%**	**41.4%**	**100%**

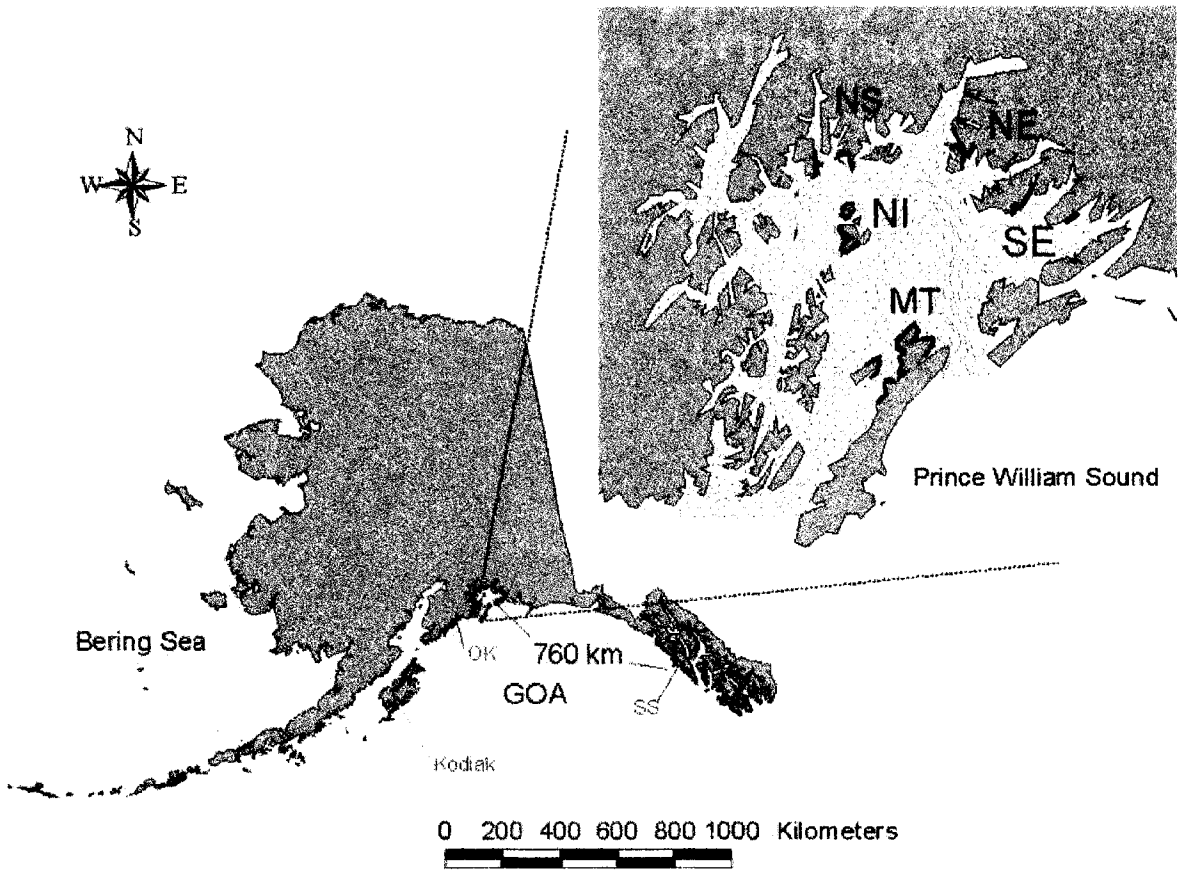

Figure 1.1. Locations of Prince William Sound (PWS), the Outer Kenai (OK), Sitka Sound (SS), Kodiak, and the Bering Sea in Alaska. Major spawning areas in PWS, including southeast (SE), northeast (NE), the north shore (NS), Naked Island (NI), and northern Montague Island (MT), and residual current structure during spawning (inset figure) are presented.

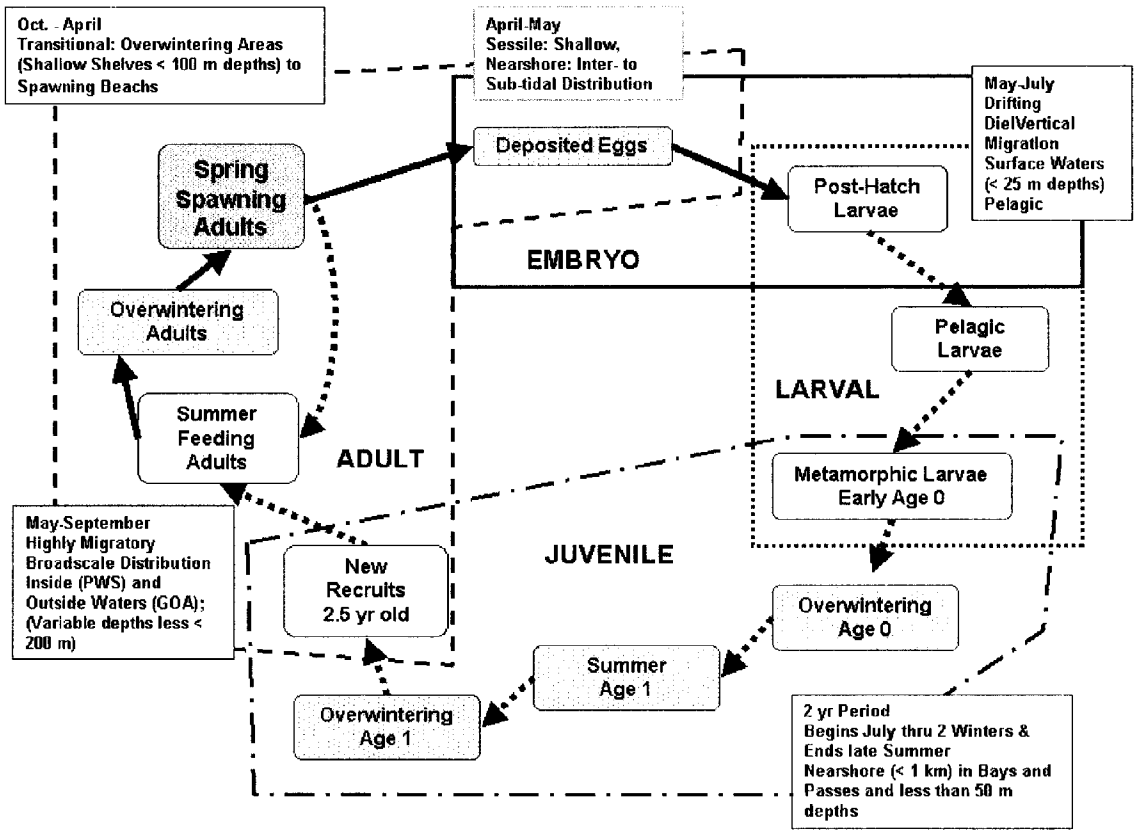

Figure 1.2. Pacific herring life history stages, stage-specific general habitat descriptions, and temporal phasing in Prince William Sound. Solid arrows delineate currently measured or modeled survival rates; dashed areas delineate unknown rates. The larger dashed polygons identify the stages included in each of the four sub-models.

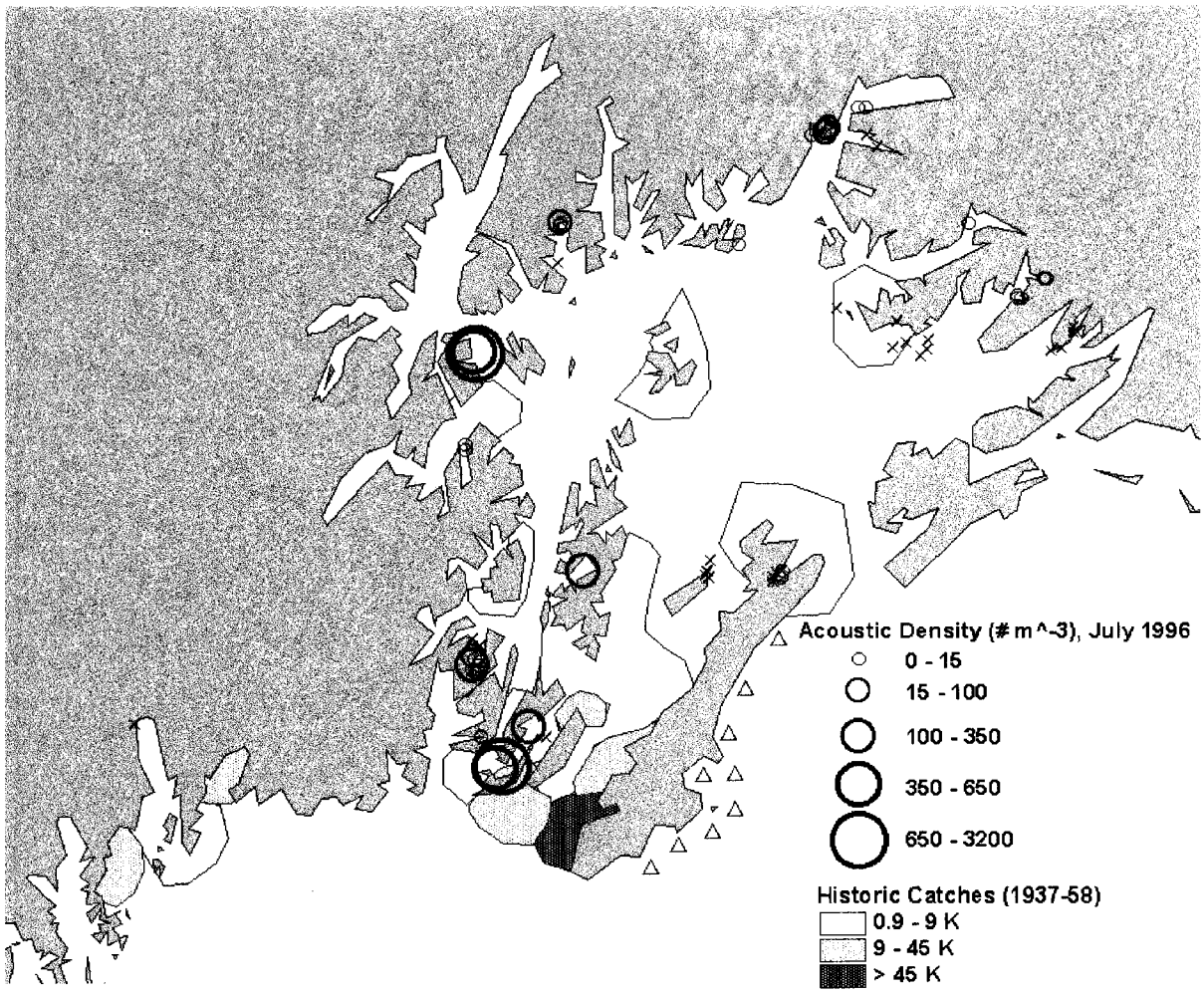

Figure 1.3. Distribution of Prince William Sound adult herring in the summer according to: 1) historic Pacific herring commerical fishing catches (thousands of tonnes; adopted from Reid 1971), 2) research collections of adults from July 1996 (abundance not estimated; shown as Xs), 3) relative abundance estimates by acoustics from July 1996 (open circles; Stokesbury et al.1999b), and 4) subset of adult herring school locations from aerial surveys in July 1996 (Norcross et al. 2001).

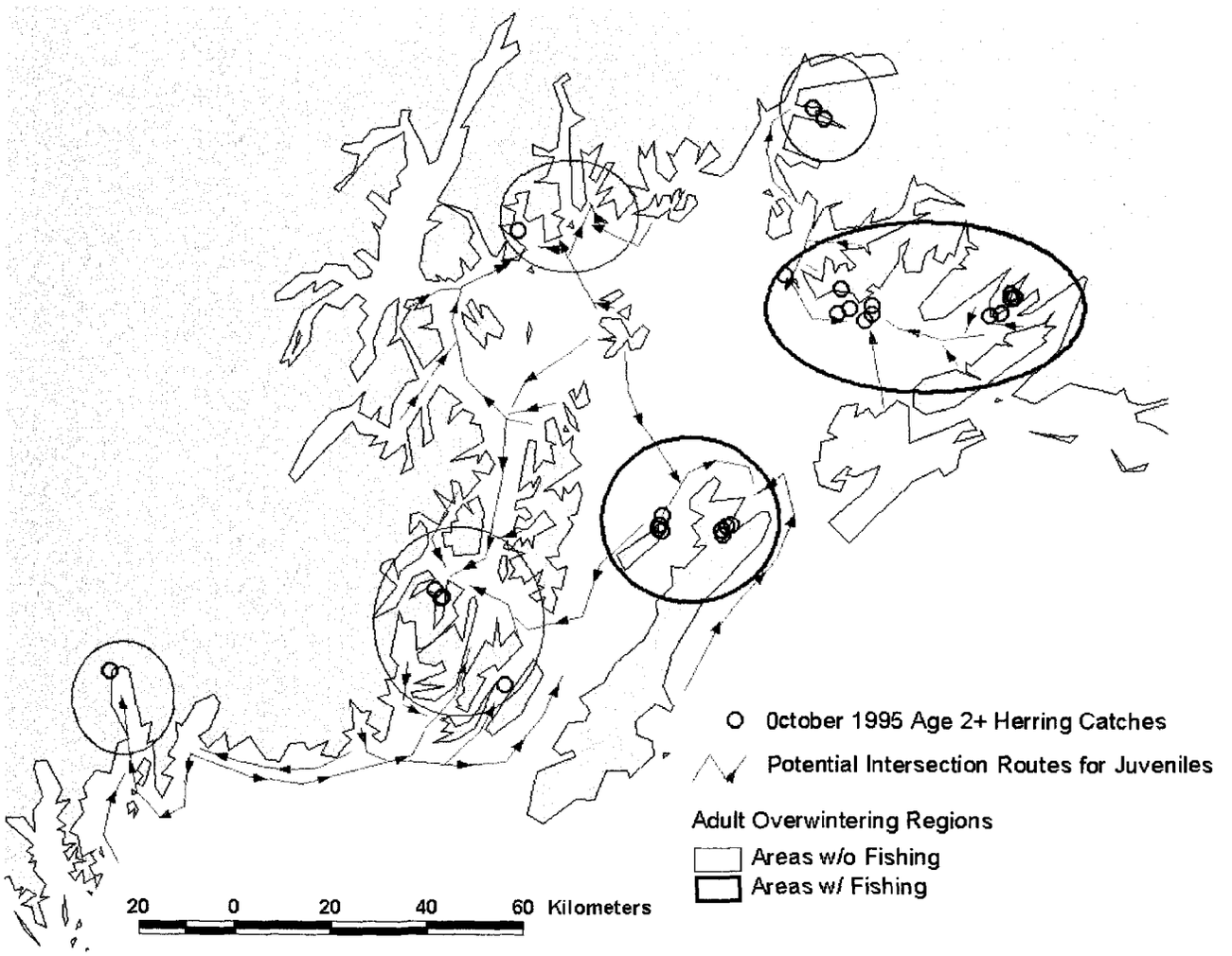

Figure 1.4. Locations of adult herring from research collections in October 1995 (small circles; Stokesbury et al. 1999a) and adult overwinter areas with historic fall-winter commerical fishing (large ovals or circles with thick lines; Donaldson et al. 1994) or without fishing (thin lines; Stokesbury et al. 1999a). Possible routes of immature herring (exiting nursery bays) resulting in intersection with adults aggregations (arrows).

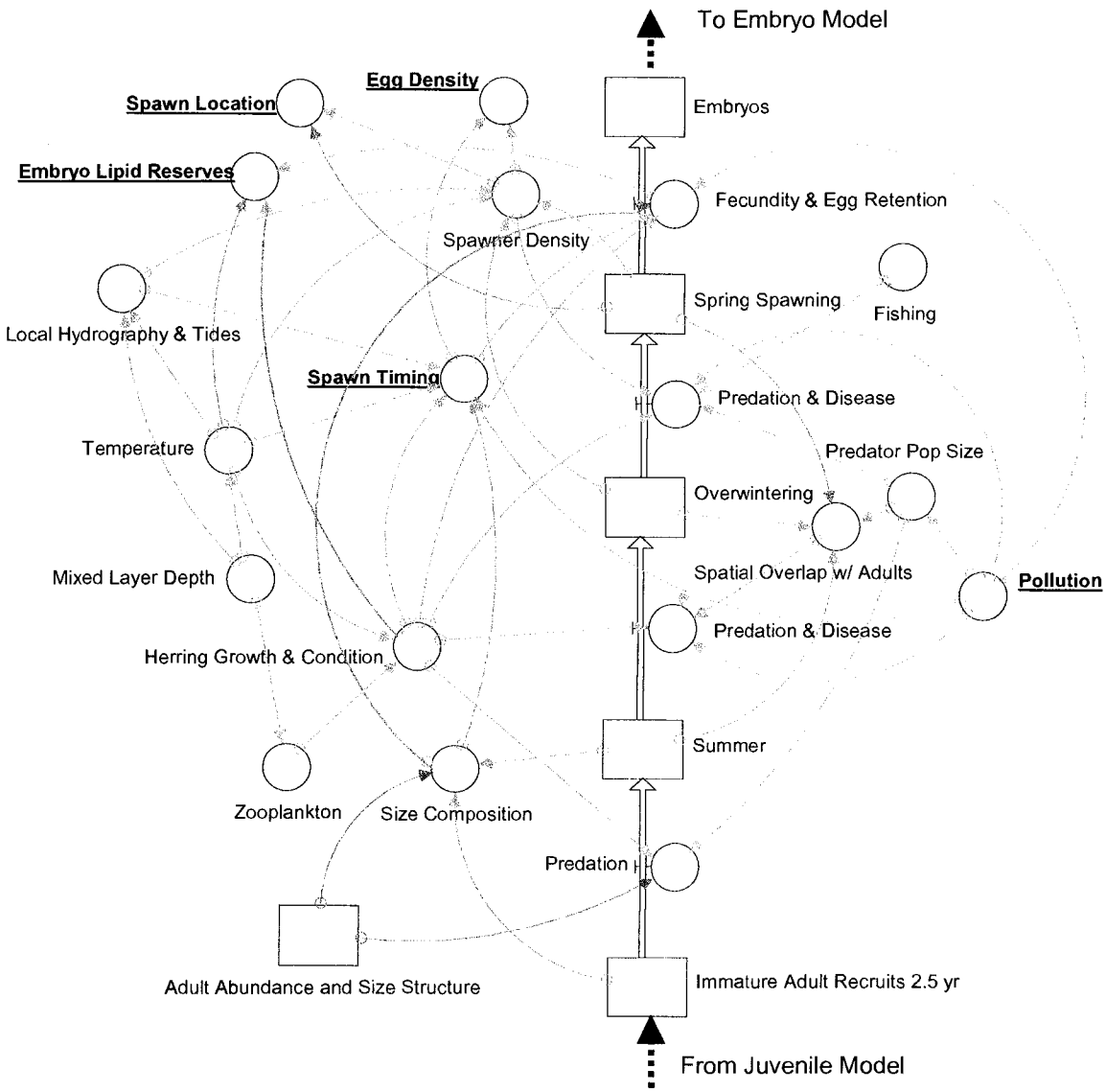

Figure 1.5. A path diagram of the adult sub-model for Pacific herring. Boxes represent the state variables of abundance and associated data of location. Hollow arrows are the flow in terms of survival and change in location between stages. Attached circles are the direct regulators of survival. Circles represent rate modifiers that directly or indirectly influence regulators or are influenced by the state variables (density dependence). The direction of the arrows indicates the direction of influence. Circles with bold and underlined text are modifiers that carry to the next stage or that are brought from the previous stage.

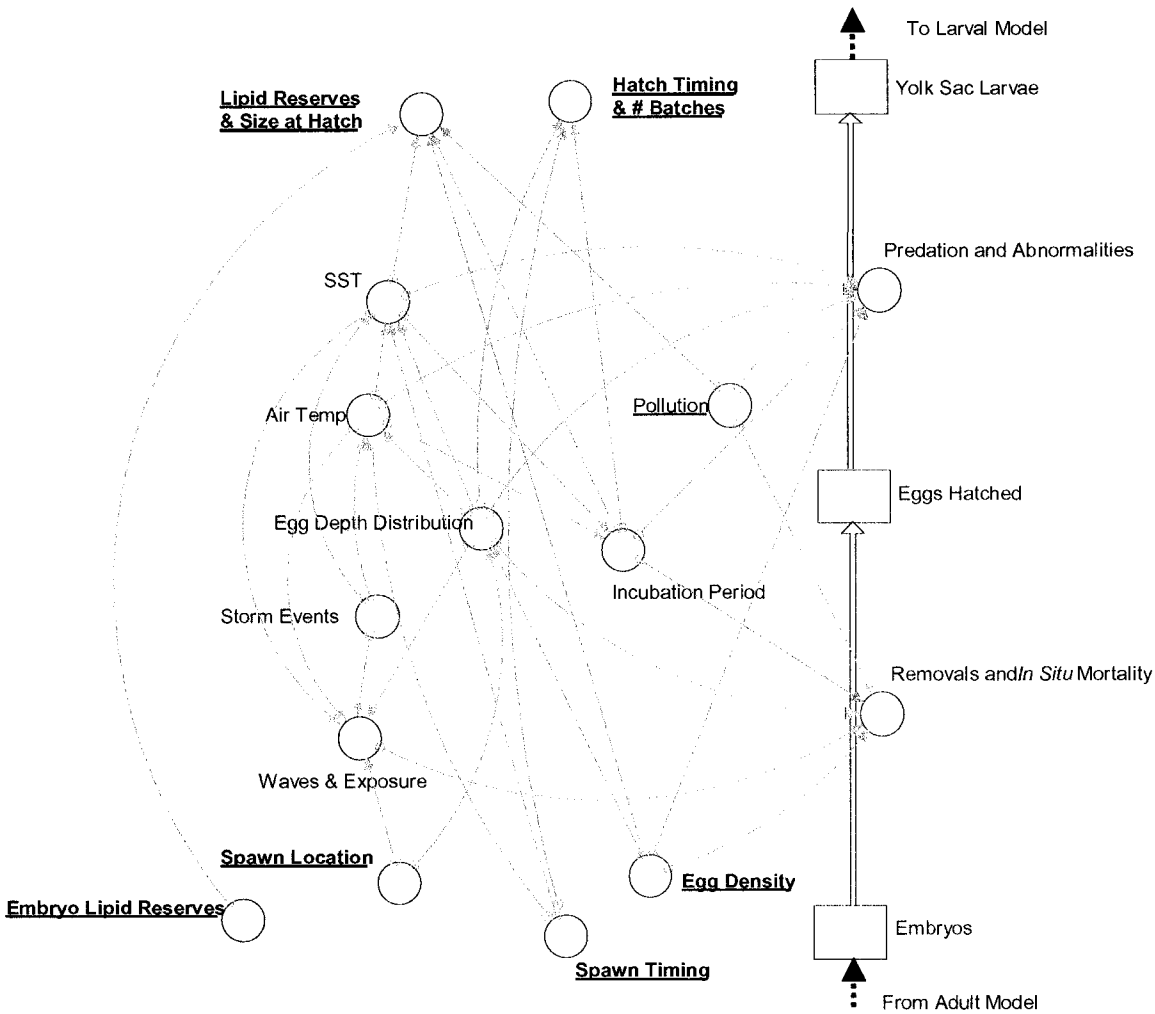

Figure 1.6. A path diagram of the embryo sub-model for Pacific herring.

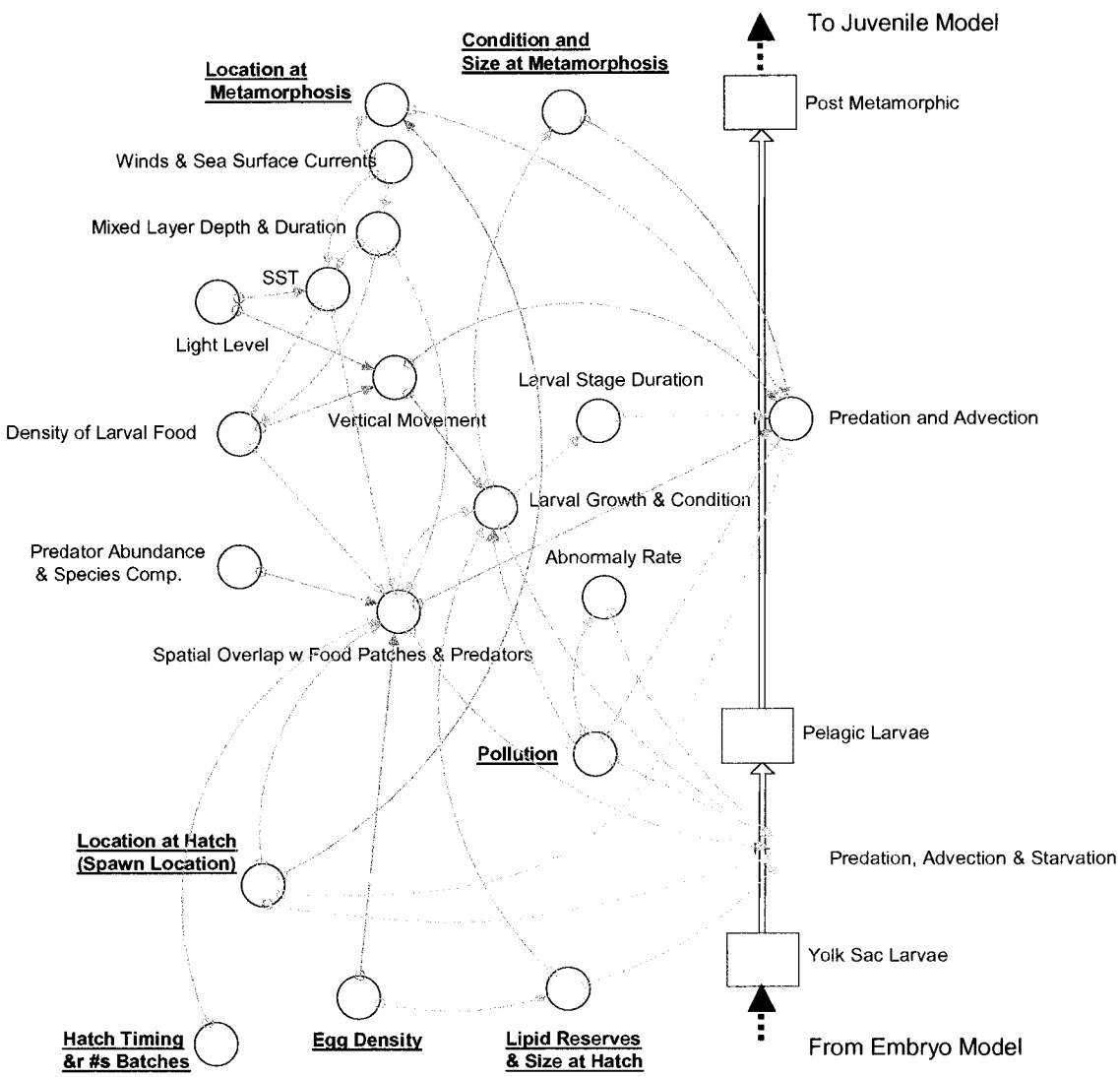

Figure 1.7. A path diagram of the larval sub-model for Pacific herring.

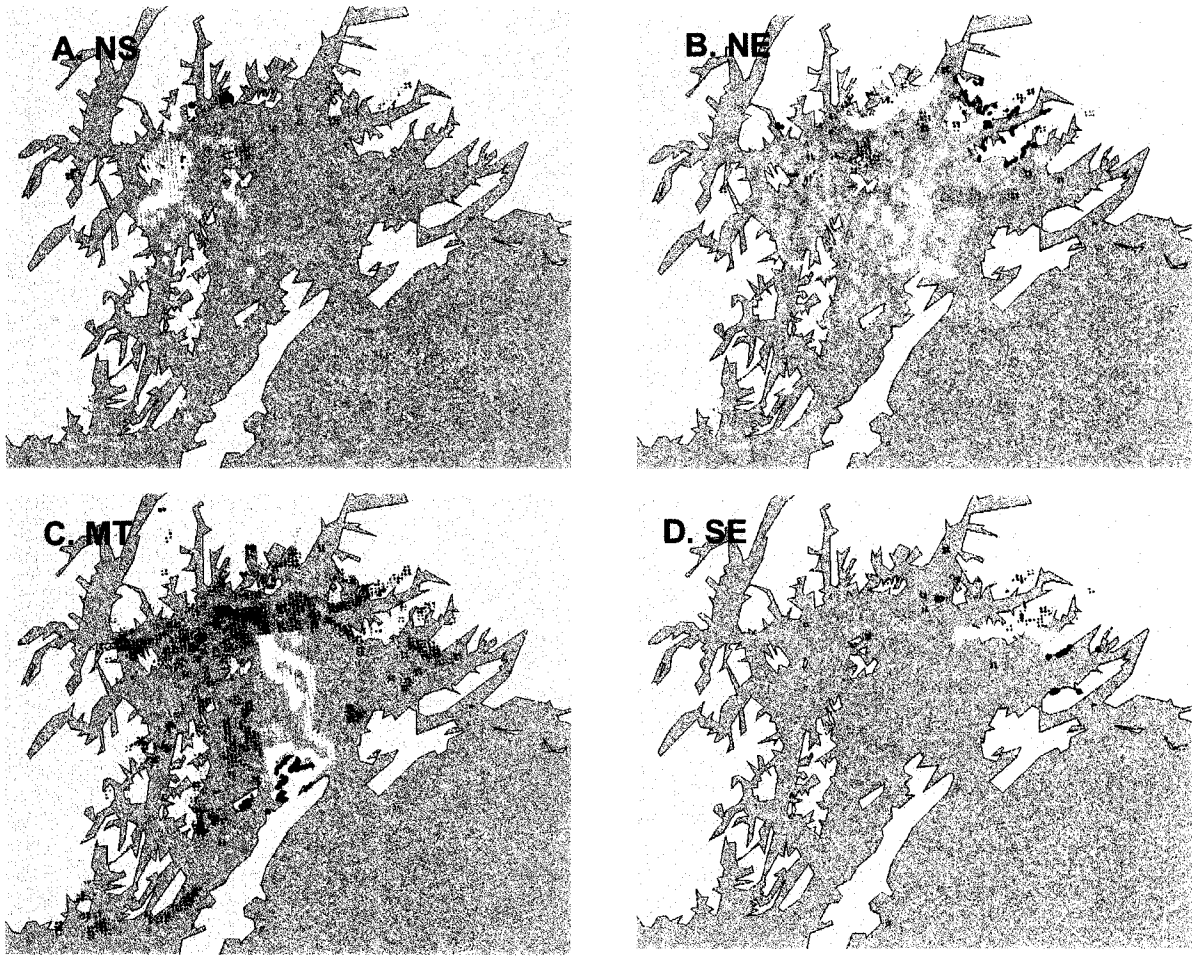

Figure 1.8. Results from a larval drift simulation (Norcross et al. In press b) showing the dispersion of larval from north shore (A), northeast (B), Montague (C), and southeast (D) spawning locations (blackened areas) as of mid-May (yellow dots), mid-June (green), mid-July (orange), and mid-August (red).

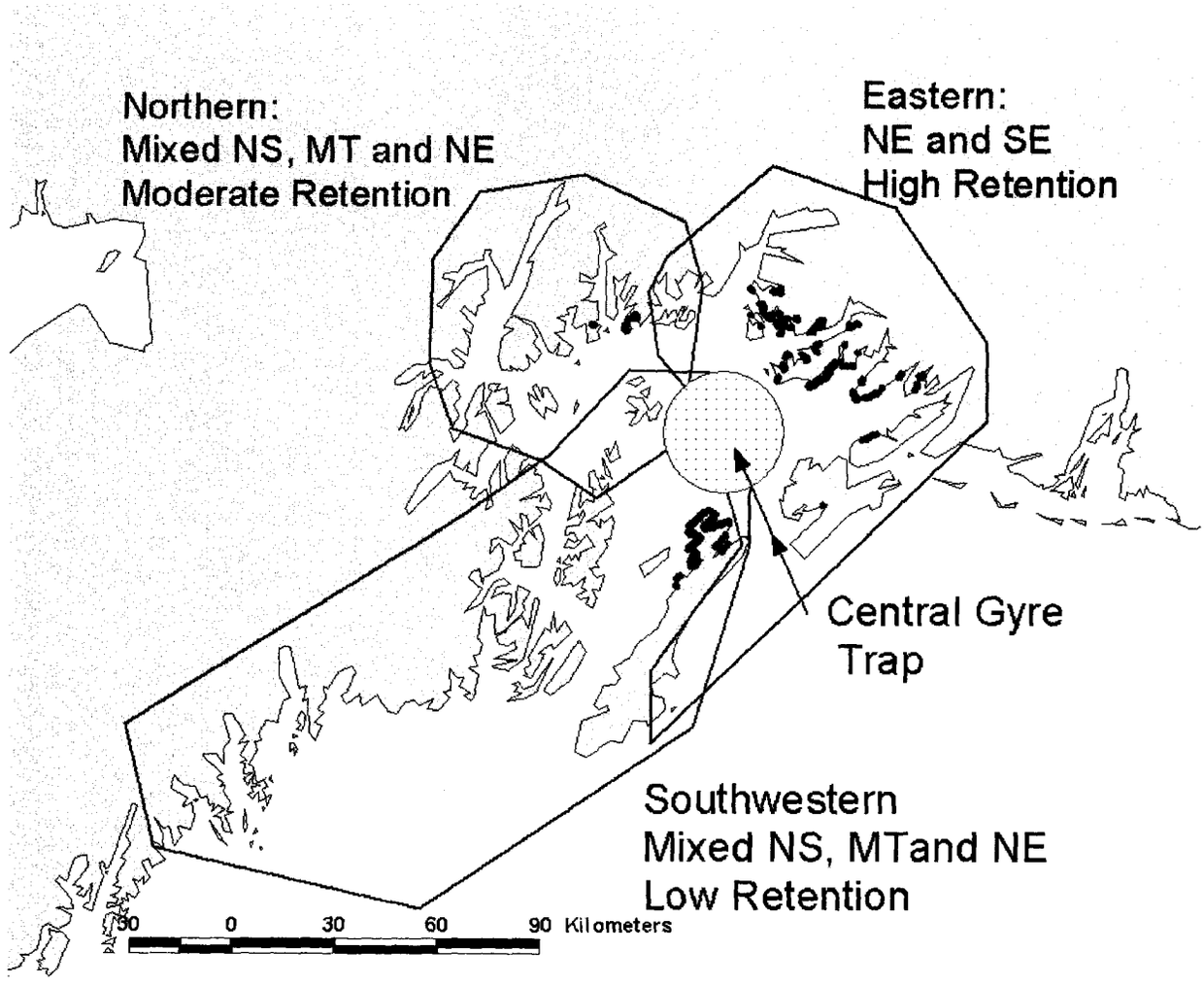

Figure 1.9. Proposed metapopulation structure for PWS comprising an Eastern local population with high larval retention, moderate vagrancy, and low migrancy; a Southwestern local population with low retention, high vagrancy, and high migrancy, and a possible third group in the North that possesses a non-migratory local population with moderate retention, moderate vagrancy, and moderate migrancy. The central gyre or theoretical "trap" is shown at the center. A composite of recent spawning locations (1995-98; John Wilcock, ADFG, unpublished data) are shown in black.

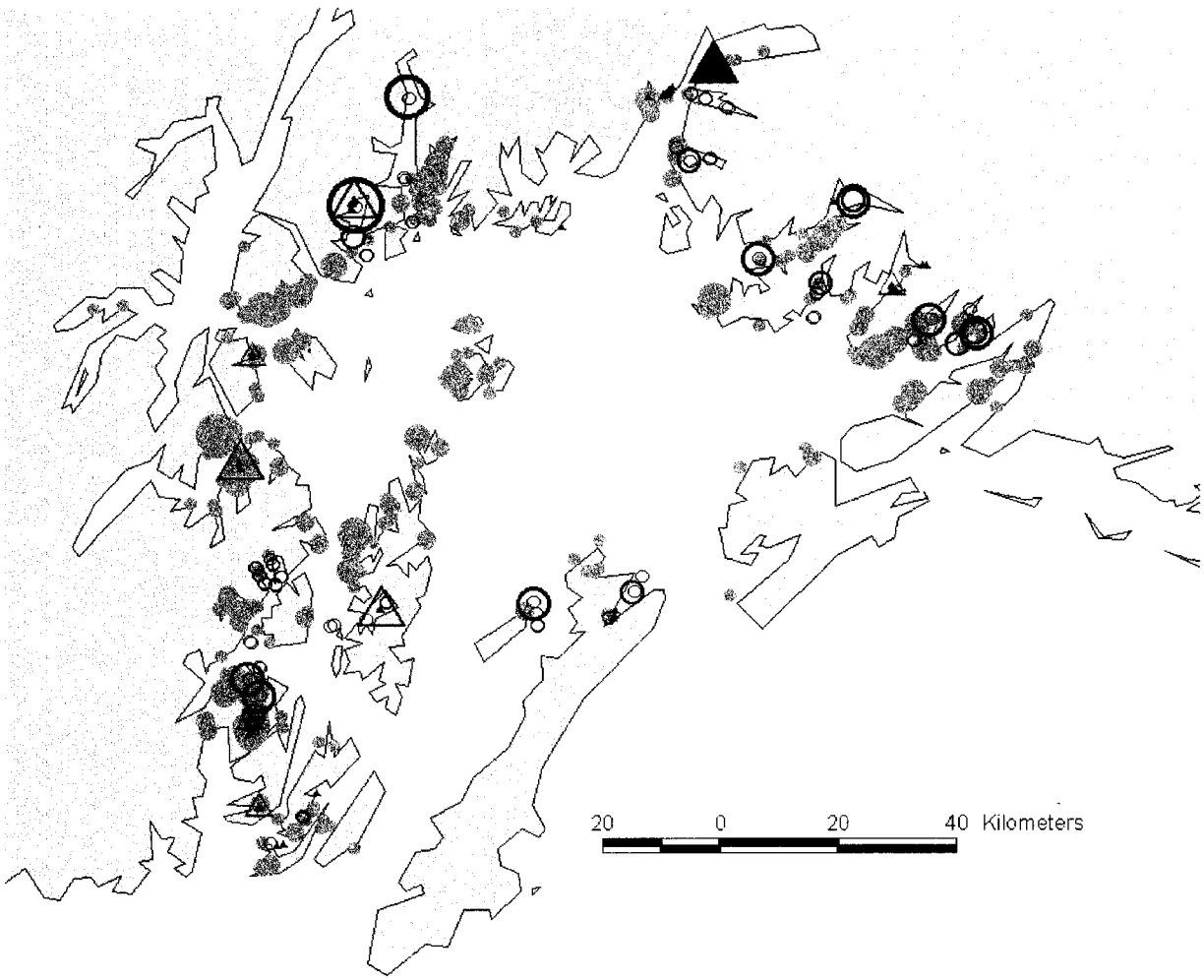

Figure 1.10. Relative catch size of pre-metamorphic herring larvae in July, 1996 (open black circles), relative abundance of age-0 (closed blue triangles) and age-1 (open red triangles) juvenile herring measured with acoustics in July 1996 (Stokesbury et al. 1999a), and relative abundance of mainly age 1 surface schooling herring (gray closed circles) from a broadscale aerial survey in July 1996 (Brown et al. In press).

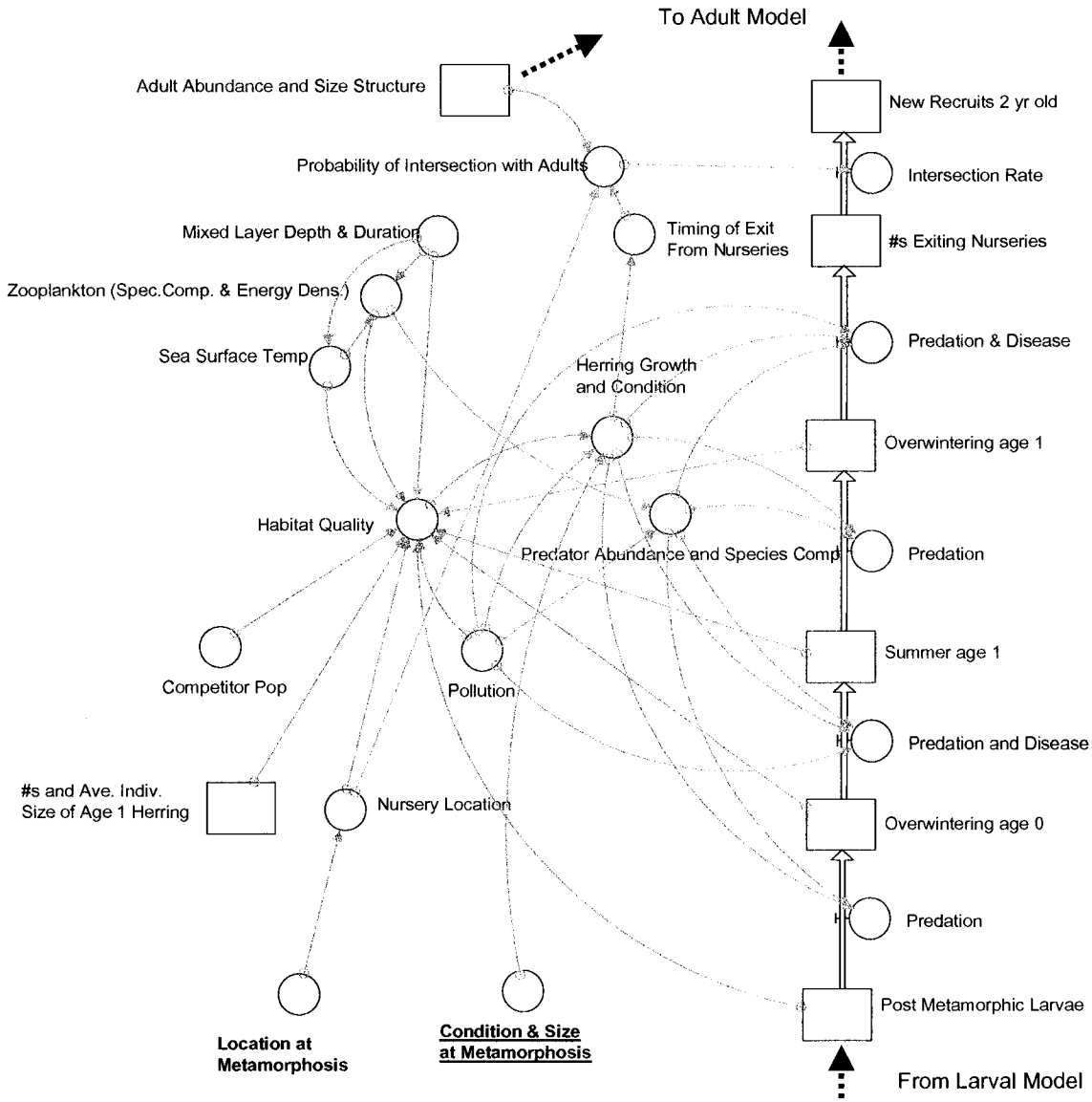

Figure 1.11. A path diagram of the juvenile sub-model for Pacific herring.

Chapter 2. Effects of climate on Pacific herring, *Clupea pallasi*, in the northern Gulf of Alaska and Prince William Sound, Alaska[1]

1. Authors E.D. Brown and F. Funk. Submitted to the Alaska Fishery Research Bulletin, November 2003. Currently in review.

Abstract

Throughout the 1900s, the abundance of Pacific herring (*Clupea pallasii*) in the northern Gulf of Alaska tracked with long-term climate trends, for example the Pacific Decadal Oscillation. Growth in adult herring from PWS was oscillatory over a 13 yr period, in phase with climate-induced zooplankton production, and was not density dependent. The mean date of spawning was correlated to fall SST and occurred progressively earlier from the early 1970s through the 1990s. Concurrently, there was a shift in major spawning use area. The production of herring recruits per spawner also decreased over this time period. This decrease in herring production may have been due to climate change, spawning area shift or both. These results supported the hypothesis that climate-induced, bottom-up forcing strongly influence Pacific herring growth and survival and that population are responding to climate-driven changes in ocean conditions.

Introduction

The link between trends of North Pacific fish populations and climatic variation is well documented (Beamish 1993; Hollowed and Wooster, 1995; Mantua et al. 1997; McGowan et al. 1998; Beamish et al. 1999; Hare and Mantua 2000). Exceptional salmon production along the North Pacific occurr during a period associated with an intensified Aleutian Low (Beamish 1993). Pacific salmon production also is strongly correlated to the Pacific Decadal Oscillation (PDO) and there is an opposite response in Alaska from West Coast (California, Oregon and Washington) stocks (Mantua et al. 1997). Alaskan

stocks appear to respond positively to the positive phases of the PDO while West Coast stocks respond negatively.

Pacific herring (*Clupea pallasii*) respond to climate similarly to salmon but differently than other forage fish species. A negative correlation exists between southern British Columbia (BC) herring year-class strength and warm conditions; warm conditions appear to reduce zooplankton food resources and increase piscivory on herring (Ware 1992). The same inverse relationship is reported by Hollowed and Wooster (1995) with higher average recruitment for Vancouver Island herring during cool years associated with a weakened winter Aleutian Low. However, the opposite effect occurs in northern BC and the Gulf of Alaska (GOA) with increased herring production during warm years associated with an intensified winter Aleutian Low (Hollowed and Wooster 1995). Pacific herring appear to have a similar north versus south opposing response to that observed in Pacific salmon. In Alaska, recruitment of Southeast Alaska Pacific herring is positively associated to warm, wet climate conditions (Zebdi and Collie 1995). Furthermore, synchronicity in herring recruitment patterns corresponds to hydrographic domains in the NE Pacific (Zebdi and Collie 1995) as originally hypothesized by Ware and McFarlane (1989). In the GOA, Pacific herring may be out of phase with other forage species, including capelin (*Mallotus villosus*) and shrimp, which appear to do better during the cool phases associated with a weakened Aleutian Low (Anderson and Piatt 1999).

In this analysis, the relationship of herring in the northern GOA to climate and climate-induced productivity is examined. We test the null hypothesis:

H_n0. Herring abundance and size-at-age is not determined by climate forcing or climate induced ocean productivity.

The alternative hypothesis is:

H_a0. Bottom-up forcing exerts a strong influence on northern GOA Pacific herring growth and survival.

Corollary 1. Climate indices or climate-induced factors are correlated to herring population trends and other life history parameters.

We also test the null hypothesis:

H_n1. Herring growth is density dependent and growth affects recruitment.

The alternative hypothesis is given as:

H_a1. The strong effects of climate on herring mask density-dependent growth.

To test these hypotheses, time series analysis is used to determine the correlation of climate indices, ocean conditions, and zooplankton abundance with herring population trends, size-at-age, and recruit-per-spawner production. Size-at-age is compared with spawning stock biomass to detect density-dependence. Finally, climate factors and herring recruitment are compared with spatial and temporal trends in herring spawning to detect an effect of climate on reproductive dynamics.

Methods

For the analysis of climate effects on population levels, data were used for Pacific herring populations in the Northern GOA, including all areas bordering the GOA from Southeast Alaska to the Alaska Peninsula (Figure 1). Data from local populations included the Alaska Peninsula, Kodiak, Cook Inlet, Prince William Sound (PWS), Lynn

Canal, Sitka Sound and Kah Shakes. For the analysis, an index of GOA herring abundance was developed spanning 1900 to 1999 using historic catch and recent catch and spawner run biomass information. Historic reduction fishery catches were available from 1900 to 1966 for all herring stocks bordering the GOA (Table 1; Figure 2). More recent fishery harvests were obtained from the same region and combined with the historic catch data (Table 1). Stock assessment programs, including estimation of the annual population-specific run biomass, were not routinely performed until after 1973 (Figure 2; Funk and Harris 1992; Funk 1995). The GOA index was derived by combining historic catch with the recent biomass estimates and forming a single series based on exploitation rates. During the peak reduction fishery (1920-1950), fishery management was virtually non-existent and exploitation rates may have exceeded 50% (Reid 1971). During the development of roe fisheries (1970s), a stock assessment and management program was initiated with exploitation rates maintained at 20% or less (Brady et al. 1991; Funk 1995). Therefore, early fishery catches are more comparable to biomass estimates than to the fishery take in latter years. The weakness of this index is the period from approximately the mid-1950s to the early 1970s when herring markets changed with a large decline in demand for herring products (Funk and Harris 1992). As a result, fishery catches and exploitation rates may have both been low and therefore the GOA index may under represent population levels during this period.

Comparisons of other population parameters, including size-at-age, spawn timing, and recruit per spawner (R/S) production, to climate signals were restricted to the PWS herring population due to availability of data. Historic records of herring age,

weight, and spawn timing were obtained for PWS (Table 1). The three main data sets used were the amount and location of spawn, the peak biomass of the spawning population (all derived from aerial surveys), and the region-specific age composition from net sampling (Table 1). Lineal beach coverage of spawn, easily observed from the air as white patches in the water, was recorded daily during the spawning period. The cumulative daily spawn coverage, reported as "mile-days" by region, represented the annual magnitude of spawn. Spawn was reported in five general regions, but regional estimates were combined into three broad areas for the analysis (Eastern, Western, and Northern; see Chapter 1) Because mile-days reflect the number of days a site receives spawn (Brady et al., 1987; Willette et al., 1998), it was a proxy measure for spawner- or egg-density. Cumulative mile-days of spawn reflected the spawning biomass. Therefore, mile-days of spawn was useful in testing population density-dependent effects. Peak aerial survey biomass was defined as the largest observed sum of estimated individual school biomass occurring over the range of spawn dates in a given geographic area. Age, weights, and lengths were measured from one or more large samples (> 600 each) of herring at each major spawning area. The proportion of biomass at each region to total biomass was used to weight the regional age compositions to obtain a PWS mean age composition. The proportion, by weight, of age 4 herring was multiplied by the total biomass to obtain and annual estimate of recruitment biomass at age 4. The age-4 biomass was divided by the total spawn for each cohort year (i.e. 4-yr lag) and log-transformed (ln) to obtain the ln R/S index for PWS.

For the comparison to PWS data, PWS mean annual sea surface temperature (SST) and salinity (SSS) measurements, down to 20 m, were calculated for each two-month interval from a wide variety of locations in PWS ($n \geq 50$ casts per location) from 1973 to 1999 (Table 1).

Climate indices and other long-term environmental data sets were compiled from a variety of sources for the GOA region. A total of 12 different physical variables were created each with monthly or seasonal components (e.g. Figure 3). Two biological variables were created representing historic zooplankton production in the northern GOA. We used the monthly anomaly of the Bakun Upwelling (UW) Index (Bakun 1973, 1975) at Hinchinbrook Entrance, just south of the eastern entrance to PWS (Table 1). The index of monthly fresh water discharge (FWD) represented an area from the southern boundary of Alaska in the southeast to Kodiak Island (Table 1; Figure 1; Royer 1982). Four wind variables were created from a site on Middleton Island (Figure 1): the monthly average wind speed, monthly variance of wind speed, average number of high speed wind events (25-35 knot gusts), and gale force events (over 35 knots). There were missing data points in the series and the last two variables were normalized as proportions to prevent bias in the mean. Significant monthly cross-correlation ($p < 0.05$) led to the reduction of wind variables to seasonal scales. The PDO, defined as the leading principal component of the North Pacific monthly sea surface temperature variability poleward of 20 ° N (Table 1), was also highly correlated among months and a seasonal index was estimated. The El Niño-Southern Oscillation (ENSO) was based on an Empirical Orthogonal Function (EOF) analysis of Sea Surface Temperature

Anomalies (SSTA) in a bounded region in the Pacific Ocean (Table 1). Two similar indices, the Pacific Inter-Decadal Oscillation (PIDO) and the Pacific Multi-Decadal Oscillation (PMDO; Table 1), represented the first and second EOF, respectively, of the residual ENSO or "non-ENSO" data set. They were correlated with the PDO. The Aleutian Low Pressure Index (ALPI) anomaly was calculated annual over a large area of the North Pacific. The Atmospheric Forcing Index (AFI) represented a combination of key climate indices (MacFarlane et al. 2000). The AFI utilized standardized scores of the first component from a principal component analysis on the ALPI, PIDO, and the northwesterly atmospheric circulation anomalies for the North Pacific (December through March). Positive values represented intense Aleutian lows, above average frequency of westerly and southwesterly winds, cooling of sea surface temperatures in the central North Pacific, and warming within North American coastal waters (MacFarlane et al. 2000). Historic zooplankton records were obtained from a "plankton watch" program performed from local salmon hatcheries in PWS (Table 1). Zooplankton settled volumes were collected from vertical tows using a 0.303-mm mesh to 30 m daily at a series of sites for a 3-mo period. However, there were many missing data points. As a result, only data from the 6-week period from mid-April to the end of May were used for this analysis. The longest time series of zooplankton values were collected in southwestern PWS, at the Armin F. Koernig Hatchery, Prince William Sound Aquaculture Corporation, on Evans Island (sampling in Elrington and Latouche Passages), and were the ones most useful in this analysis. The two variables created were annual mean and peak values of settled volume from the southwestern PWS site.

Time series methods (Diggle 1990) were used to characterize the data sets, determine multicolliearity among the physical data sets, determine significant cross-correlations between the physical and biological series, and determine prominent periods in the data. Plots of autocorrelations and partial autocorrelations were used to determine the appropriate smoothing function to reduce short-term (≤ 5 yr) noise in the biological data. The appropriate smoothing functions included moving average (ma) (Diggle 1990) and polynomial fits. Several of the climate indices were auto-correlated due to a similar base of information (e.g. SST and atmospheric factors). Cross-correlation among the AFI, ALPI, PIDO, and PDO indices were moderate to high ($r \geq 0.62$). The PDO was also correlated to 4 yr ma of January and April upwelling indexes as well as 4 yr ma of March freshwater flow. Although there were significant ($P \leq 0.10$) correlations among other variables, the r-value did not exceed 0.5. The smoothed biological series were compared with the physical indices one at a time to determine the best fit. Cross-correlation and distributed lags analysis (Fomby et al. 1984) was used to estimate the level of significance in the relationships, correlation coefficient (r), and significant lag between series. Only those relationships with a signal level of 0.10 or less were reported and the r value was presented for the best fit series Because of auto-correlation in time series analyses, p-values do not have a clear meaning as they do in other stochastic methods (Diggle 1990) and were not reported here.

Spectral analysis (Diggle 1990) was used to determine if size-at-age data was oscillatory and if so, the period and appropriate spectral smoothing function, using the Hamming transformation and window (Blackman and Tukey 1959). Size-at-age series

were then compared to other physical and biological indices to determine significant correlations. Size-at-age data were also plotted against biomass to detect density-dependence.

The log-transformed (ln) R/S production was compared to the proportion of spawn at each of three major spawning regions over time using time series regression. A similar analysis was performed on ln R/S versus the size at age for age 4 to determine the effects of herring growth on herring recruitment.

Results

Periods of high herring population were generally associated with the positive phases of the significant climate indices. The PWS spawner run biomass was significantly correlated to the four major indices (AFI, ALPI, PIDO and PDO). The highest correlation was with the winter PDO ($r = 0.75$) and obtained with a 4 yr ma smoothing applied (Figure 4). The next best fit was with the ALPI lagged 4 yrs, followed by the AFI lagged 4 yrs, and PIDO lagged one yr (not shown on figure). The GOA herring index was significantly correlated with the same four variables (Figure 5). The highest r-values were obtained with a 5 yr ma smoothing function (Figure 5a). The best fit occurred with the PIDO (0.78; Figure 5a), followed by the AFI, then ALPI, and winter PDO. These results led to a rejection of the null hypothesis that climate is not related to the northern GOA herring abundance.

Herring size-at-age trends exhibited oscillatory behavior with a maximum in spectral density at a period of 13 yrs for all ages (Figure 6). The spectral peak was strongest in ages 3-5. The raw and smoothed (using the Hamming filter) size-at-age data

were significantly correlated to peak zooplankton density anomalies lagged one year ($r \geq 0.50$; Figure 6). Peak and average zooplankton biomass was significantly correlated to the winter PDO lagged 3 yrs ($r = 0.52$ and 0.65 respectively). Size-at-age for ages 7 and 8 were also significantly correlated to both the PDO lagged 3 yrs ($r = 0.55$) and the PIDO lagged 2 yrs ($r = 0.61$). The cumulative results led to an acceptance of the alternative hypothesis that bottom-up forcing exerts a strong influence on herring growth and survival and the corollary that climate-induced factors are correlated to herring population and life history parameters.

Although size-at-age did not decrease with population size (Figure 7), indicating a lack of density-dependence at the population level, the close relationship with zooplankton and fish size (Figure 6) indicated that food limitation may occur. Given these results, the null hypothesis that growth is density dependent and impacts recruitment cannot be rejected.

Mean spawn dates were highly variable and spawning had been progressively earlier since the 1980s but similar to spawn dates in the 1970s (Figure 8). The mean spawn date anomaly was weakly correlated to the Sept-Oct. SST anomaly the fall prior to spawning ($r = 0.49$). Mean spawn date was not significantly correlated to any other climate variable.

The log-transformed recruit per spawner (ln R/S) index for age 4 herring was highly variable but exhibited a general downward over the last 26 yrs (Figure 9). During this period, spawning area use had also shifted from mainly eastern to western PWS. The ln R/S was significantly correlated to average zooplankton settled volume anomaly

lagged 1 yr (Figure 9a; r = 0.68). This corresponds to secondary production during age 1 or just prior to the 2nd birthday of the cohort. Neither the ln R/S with trend or detrended value was correlated to size-at-age. However, ln R/S was significantly correlated to the proportion of eastern spawning (Figure 9b; r = 0.66). During the 1980s, when the population was at a peak, spawn was more evenly spread among eastern, western and northern spawning beaches than in the 1970s or 1990s.

Discussion

The relationship of GOA herring to climate indices is similar to the relationships for salmon production and climate (Mantua et. al. 1997; Hollowed et. al. 1998) and GOA zooplankton production (Brodeur and Ware, 1992; Brodeur et al. 1996). In the subarctic, a strong Aleutian Low causes above-average fall and winter water column mixing, with a high influx of nutrients, followed by above-average spring to summer stability creating conditions that optimize primary and secondary production. The scenario is a direct application of the optimal environmental window theory (Cury and Roy, 1989) where a domed shaped relationship exists between wind-induced upwelling and recruitment due to nutrient limitation of primary production during periods of low upwelling versus excess turbulence during intensified upwelling. This may be the mechanism involved in the positive response of zooplankton and Alaskan Pacific salmon stocks to a positive PDO signal (Gargett, 1997). Because GOA herring react similarly to climate, the mechanism may be the same for herring. Enhanced zooplankton resources likely result in higher growth and possibly better survival for early life stages

of herring. In this case, we were able to directly relate the recruit per spawner production to zooplankton (Figure 9b).

Periods of high herring production were associated with periods of positive PDO and AFI index values (Figures 4 and 5). The two peaks in abundance in the GOA, during the 1930s and 1980s, correspond to similar peaks in the PDO. There was not a corresponding peak in the 1960s. However, this may be due to poor information during the 1960s rather than a lack of relationship. Stock assessment programs were non-existent and fishery catches were low due to weak herring markets (Reid 1971). It is possible that herring were more abundant than indicated, as they were in the Bering Sea during this period (Wespestad 1991). If so, the overall correlation between population level and climate could have been even stronger.

Evidence for this climate-driven relationship between zooplankton and growth is evident in the cyclic herring size-at-age pattern and significant correlation to peak levels of zooplankton density (Figure 6). In addition, size-at-age was oscillatory over a decadal scale (13 yr) period. The lack of density dependence evident at the population level (Figure 7) does not eliminate the possibility for density-dependent affects on growth. The apparent food limitation, given the relationship between fish size and zooplankton (Figure 6), indicates that density-dependent processes could occur. It is likely that these processes occur at the scale of individual herring aggregations and are therefore uncorrelated with the population size during the cohort year. Since zooplankton is responding to cyclic climate patterns, a similar cyclic pattern is induced in herring size at age.

There was no observed effect of growth on recruitment success, measured as adult size-at-age and year-class strength. However, a relationship might not be expected if year-class strength is determined in the first year. In that case, size-at-age of age 3 and older herring would reflect only the growth history of the survivors and mask the overall growth affect on recruitment.

The relationship between SST 6 mo prior to spawn and the mean spawn date (Figure 8) agrees with other studies on Pacific herring. Spawn timing is a function of the temperature exposure history of the adults (Hay 1985; Hay and Kronlund, 1987; Ware and Tanasichuk 1989; Wespestad 1991) as well as the age composition since older, larger herring spawn earlier (Hay 1985; Ware and Tanasichuk 1989). Because of the relationship between spawn timing and age composition, spawn timing should be highly variable due to variations in SST and the arrival of a recruiting cohort every few years. Herring exhibit plasticity in maturation rates and spawn timing as an adaptive process in response to changing ocean conditions (Lasker 1985; Winters and Wheeler 1996; Sinclair 1988). Therefore, spawn timing should generally follow ocean conditions, especially temperature.

In PWS, the links between the declining R/S trend, the east to west spawn area shift (Figure 9a) and climate-driven trends in ocean conditions are not well understood. The shift in spawning region may simply represent a random switch. Alternatively, the shift in spawning area could be a function of climate-driven changes in ocean conditions favoring the choice of one area over another. The actual cause of the decline deserves further examination.

In summary, GOA herring populations are responding to climate-driven changes in ocean conditions. The implication for fishery management is that stock protection or building measures can only operate up to stock levels dictated by climate. Because herring play an important role in the northeast Pacific ecosystem, changes in population levels could potentially impact apex predator or herring competitor population levels. Ecosystem modeling of process-oriented responses of herring to ocean conditions (e.g. model in Chapter 1) could be a useful tool for interpreting the relationships found in this analysis.

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Table 2.1. Types and sources of data used to determine the effects of climate on herring in the Northern Gulf of Alaska and Prince William Sound.

Data Type	Time-Frame	Sources
Historic fishery harvests	1900-1966	Skud et al. 1960; Reid 1971 Gretsch et al. 1989; Prokopowich 1989; Schroeder and Morrison 1989; Brady et al. 1991; Larson and Minnicucci 1991; Funk and Harris 1992
Recent fishery catches and stock assessments	1973-1999	Fritz Funk, ADF&G Juneau, personal communication; web site: http://www.cf.adfg.ak.us/geninfo/finfish/herring
Total Annual PWS Spawn in mile-day	1973-1999	Biggs et al. 1992; Brady *et al.* 1987 Steve Moffit and John. Wilcock, personal communications, ADFG, Cordova; Fritz Funk, ADF&G Juneau, personal communication
Age 3 and 4 recruitment biomass and regional age composition measurements	1973-1999	
Bakun Upwelling Index	1946-1999	Bakun 1973, 1975; http://www.pfeg.noaa.gov/products/
Fresh water discharge	1931-1999	Royer 1982; University of Alaska (UAF), Institute of Marine Science (IMS) database
Middleton Island meteorological data	1972-1999	National Climate Data Center, North Carolina
Precipitation and air temp. PWS sites	1972-1999	
Pacific Decadal Oscillation (PDO)	1900-1999	Mantua et al. 1997
El Niño-Southern Oscillation (ENSO)	1870-1998	Enfield and Mestas-Nuñez, 1999
Pacific Inter-Decadal Oscillation (PIDO)	1856-1998	
Pacific Multi-Decadal Oscillation (PMDO)	1856-1998	
Aleutian Low Pressure Index (ALPI)	1901-1998	Beamish and Bouillon, 1993
Atmospheric Forcing Index (AFI)	1900-1999	MacFarlane et al. 2000
Historic zooplankton	1980-1999	Prince William Sound Aquaculture Corporation (Cordova, Alaska) plankton watch program
PWS hydrographic data	1973-1999	UAF IMS database

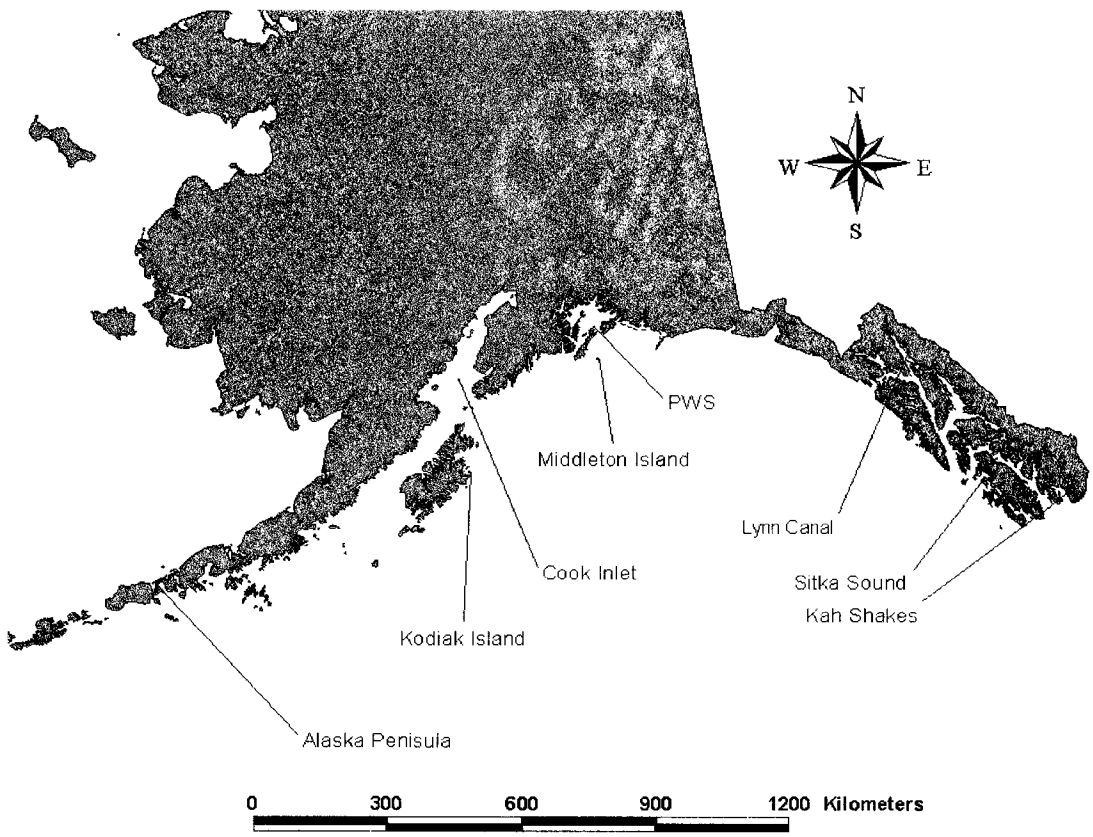

Figure 2.1. The Gulf of Alaska (GOA) region covered in this analysis.

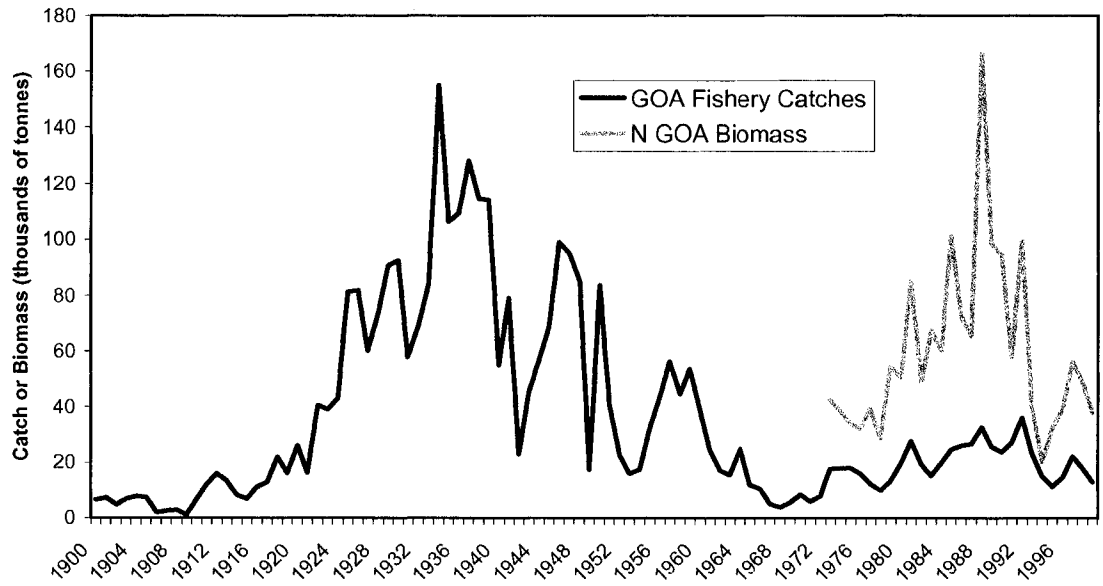

Figure 2.2. The two types of fishery data used in this analysis. The solid black line is total annual Gulf of Alaska (GOA) fishery catches from the GOA region (Skud et al. 1960; Reid 1971; Gretsch et al. 1989; Prokopowich 1989; Schroeder and Morrison 1989; Brady et al. 1991; Larson and Minicucci 1991; Funk and Harris 1992; unpublished catch records from Fritz Funk, ADF&G, Juneau, Alaska). The grey line represents the annual biomass estimates for Prince William Sound in the northern GOA (Funk and Harris 1992; unpublished stock assessment records from Fritz Funk, ADF&G, Juneau, Alaska).

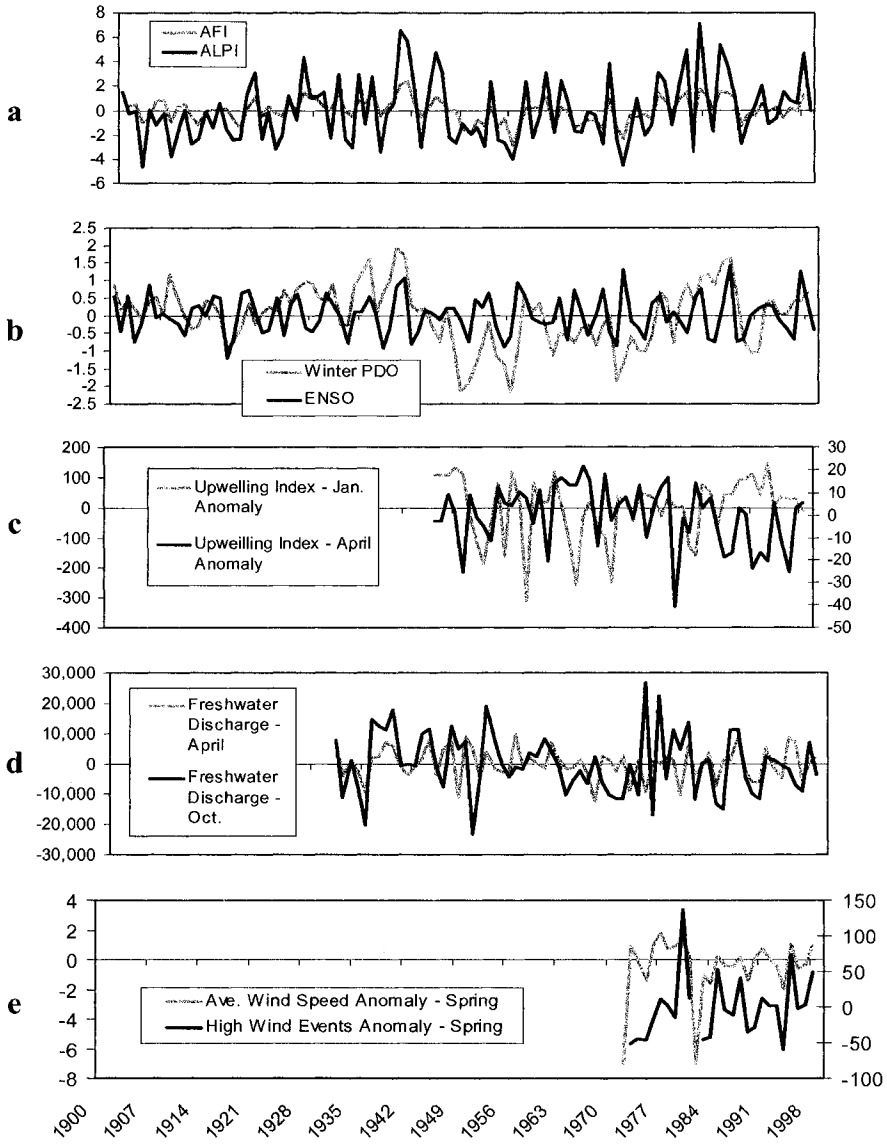

Figure 2.3. Examples of long-term climate data sets used in this analysis: a) the Atmospheric Forcing Index (AFI) and the Aleutian Low Pressure Index (Beamish and Bouillon 1993; MacFarlane et al. 2000), b). the winter Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and the El Niño Southern Oscillation (ENSO; Enfield and Mestas-Nuñez 1999), c). the Bakun upwelling index anomaly for January and April (Bakun 1973, 1975), d). an index of freshwater discharge for April and October (Royer 1982), e). average wind speed anomaly and high wind event (average number of events between 25 and 35 knots) anomaly at Middleton Island, northern Gulf of Alaska (U.S. National Climate Data Center).

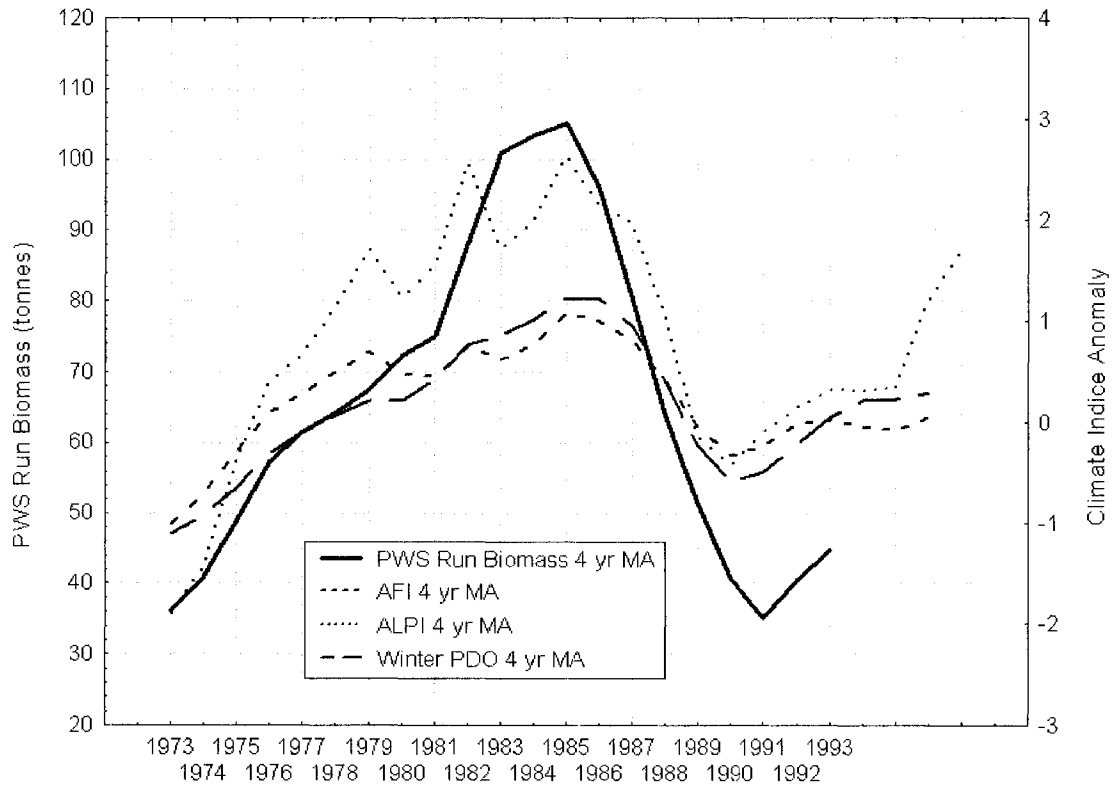

Figure 2.4. A 4 yr moving average (ma) transformation of the PWS biomass index compared to the AFI (lagged 4 yrs), the ALPI (lagged 4 yrs) and the winter PDO (no lag) for the period of 1973 to 1993.

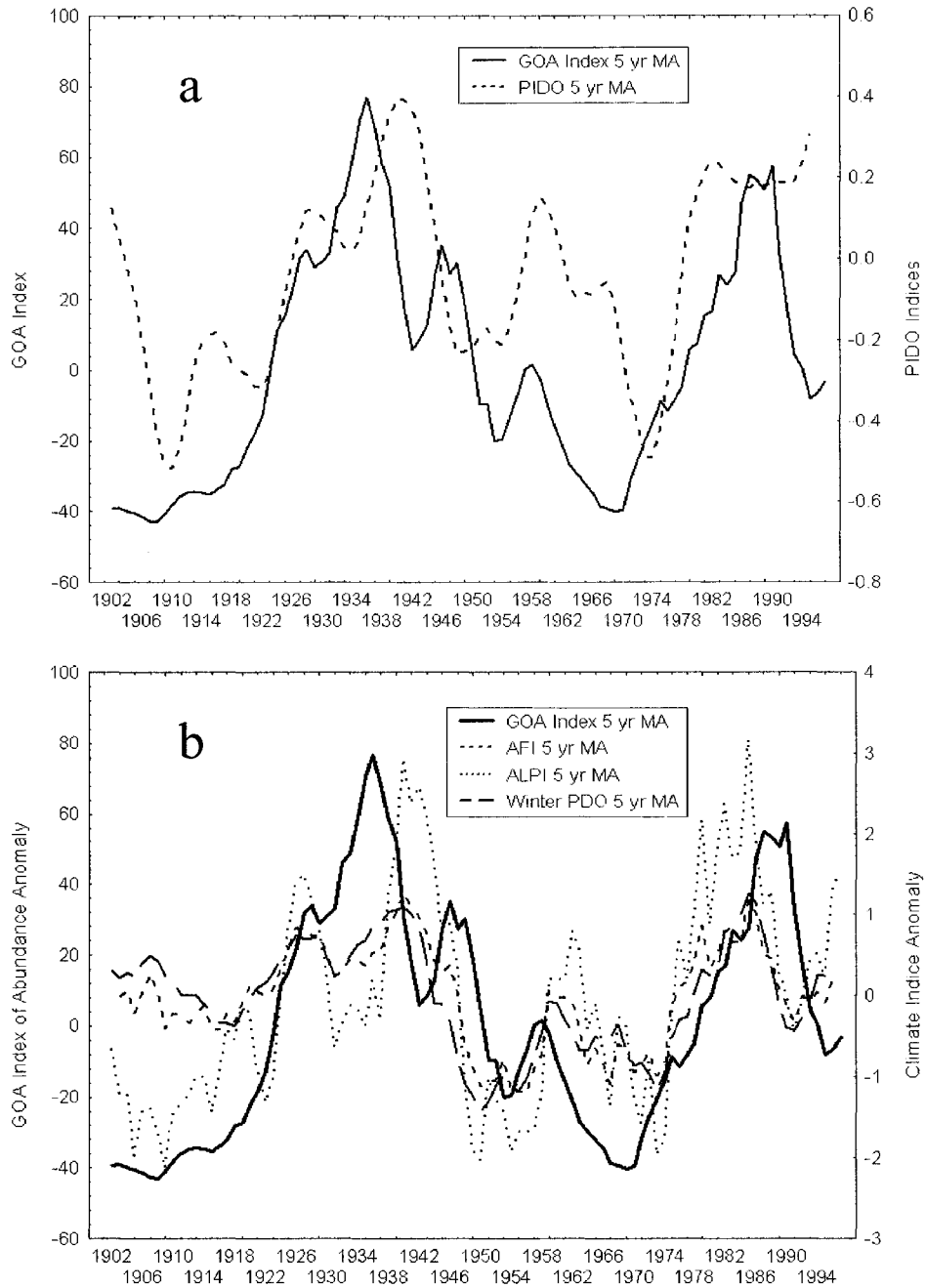

Figure 2.5. A 5 yr moving average (ma) of the Gulf of Alaska (GOA) Index of herring abundance, created by combining catch and biomass, compared to a 5 yr ma of the Pacific Inter-Decadal Oscillation (a; Enfield and Mestas-Nuñez 1999) and and 5 yr ma of the GOA Index, AFI, ALPI and winter PDO plotted for the period of 1902 to 1995 (b).

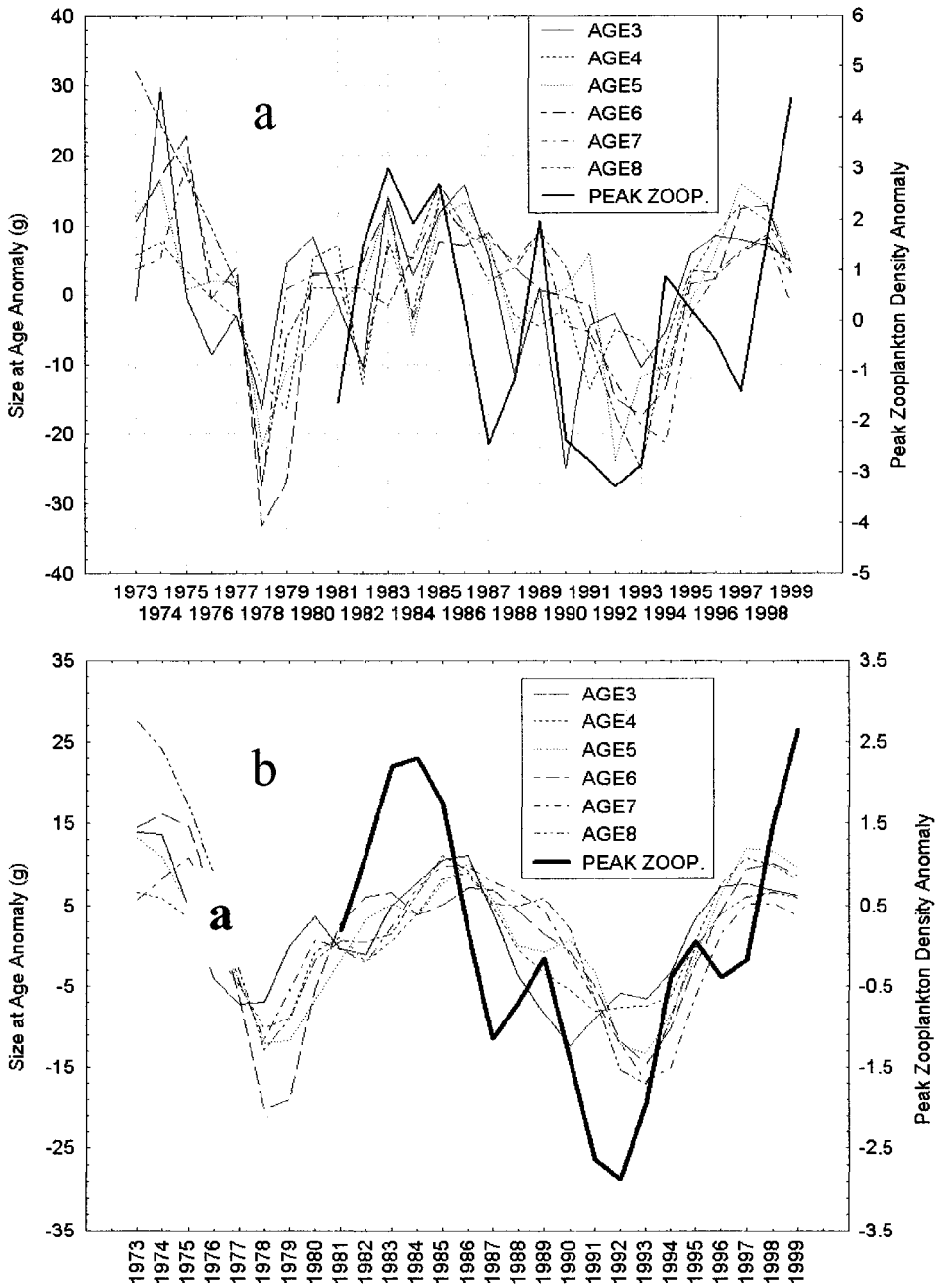

Figure 2.6. Size-at-age by weight (g) of age 3-8 Pacific herring from PWS are significantly correlated with peak zooplankton density anomalies (from southwestern PWS) for the period of 1973 to 1999 whether as raw values (a) or as a spectral transformation (type Hamming) of the size-at-age data plotted with a 4 yr moving average transformation of peak zooplankton anomalies (b).

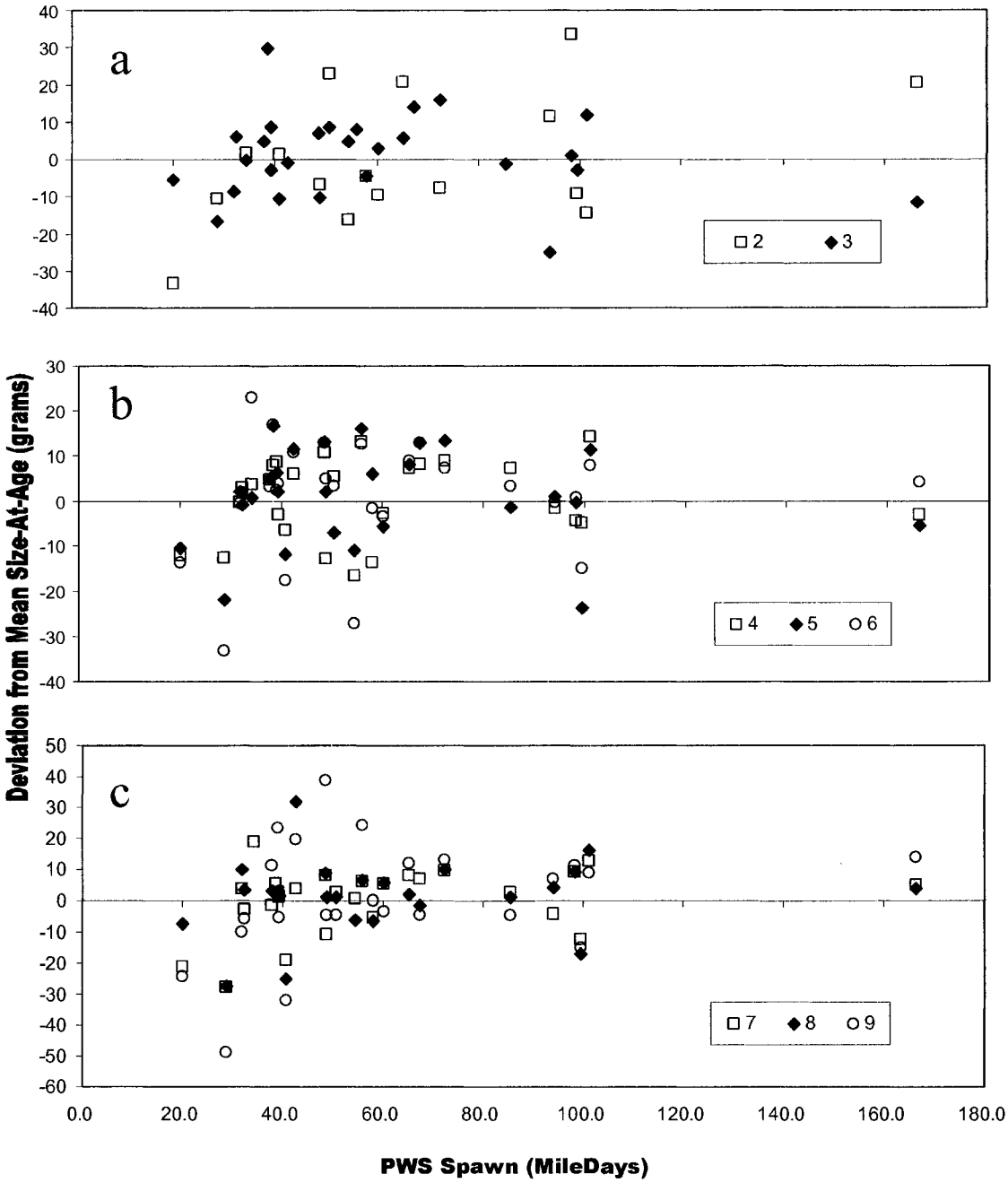

Figure 2.7. The PWS herring size-at-age anomaly (grams) is not significantly correlated to the PWS spawner abundance (proxy measurement is total spawn) at any age. Shown are Ages 2-3 (a), 4-6 (b) and 7-9 (c).

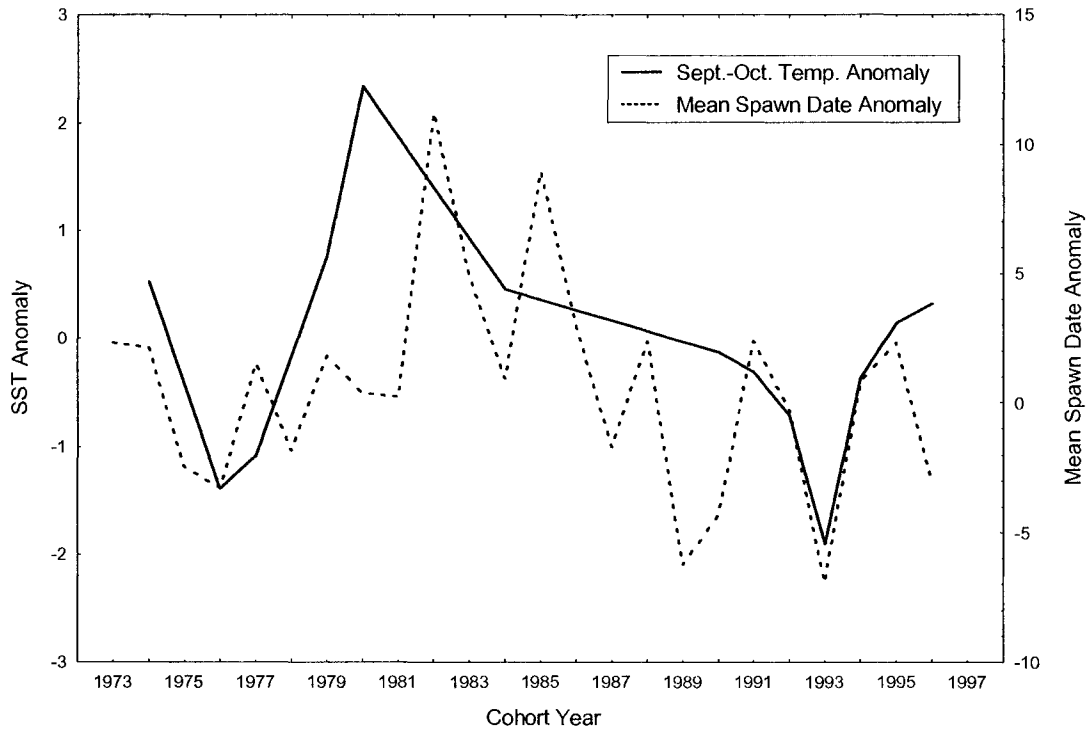

Figure 2.8. The smoothed series for the September-October (6 mo prior to spawning or cohort year) mean sea surface temperature (to 20 m) anomalies plotted with the mean date of spawning anomaly for PWS for the period of 1973 to 1999. The time series correlation is weak but significant.

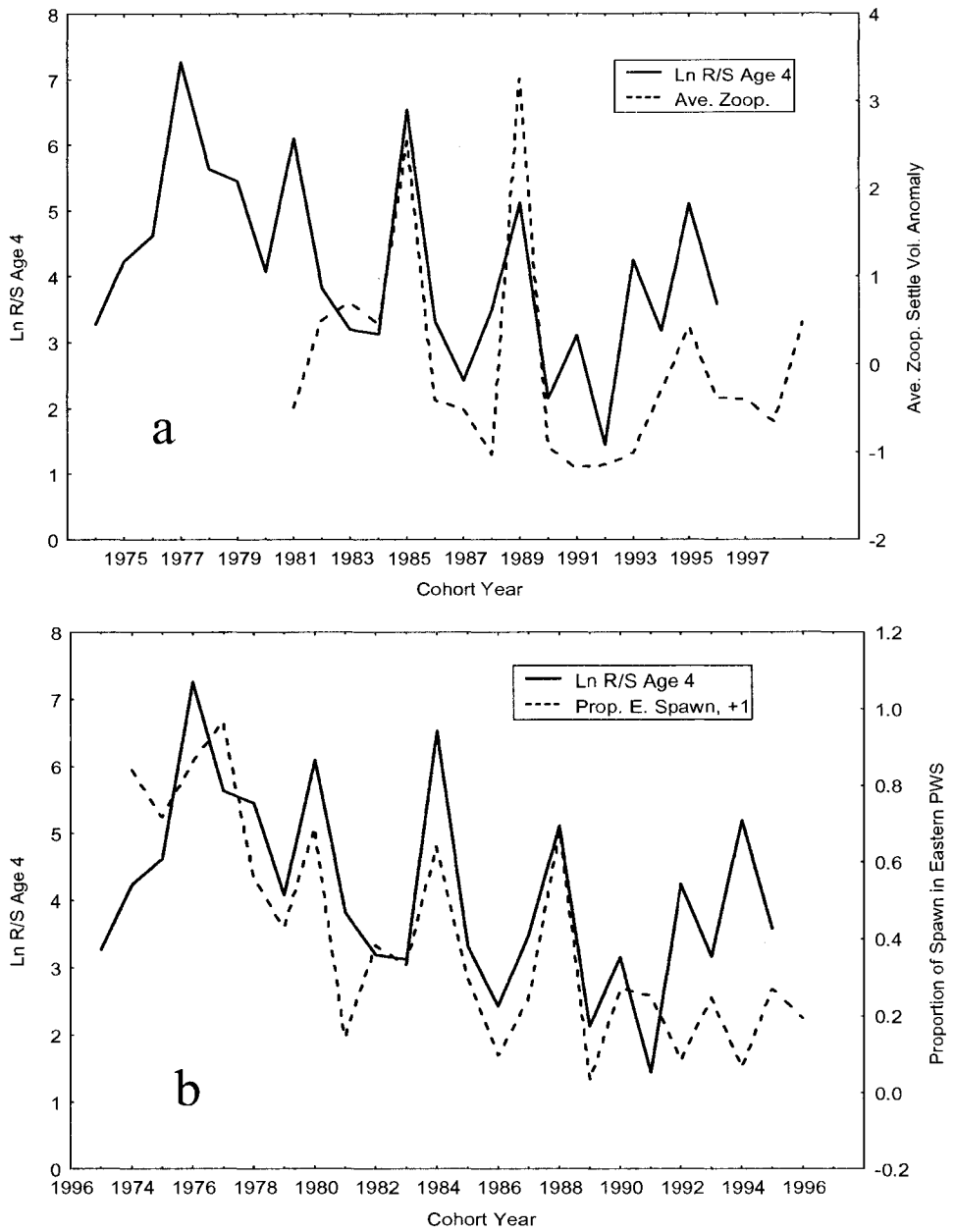

Figure 2.9. The natural log transformation of the recruit per spawner (ln R/S) index for PWS is significantly correlated with with average zooplankton density anomaly (a corresponding to age 1 herring around their first birthday. The ln R/S index (lagged 1 yr) is also significantly correlated the proportion of spawning (by lineal coverage on the beach) occurring Eastern PWS for the period of 1973 to 1995 (b)

Chapter 3. Effect of Environmental Factors and Spawn Distribution on Regional Recruitment of Pacific herring, *Clupea pallasi*[1]

1. Authors E. D. Brown and B.L. Norcross. To be submitted to Transactions of the American Fisheries Society.

Abstract

Environmental recruitment models were developed to improve recruitment models for Pacific herring (*Clupea pallasi*) in Prince William Sound (PWS) given the weak stock-recruitment relationship. Models were improved by accounting for stock structure, including three local regions (eastern, northern, southwestern) and applying appropriately scaled local environmental variables over monthly or seasonal periods. Critical life history periods were defined by identifying lags and seasons with the best model fits. Generalized additive modeling was used to maximize flexibility in determining functional relationships. The best-fit environmental recruitment models explained up to 91% of the variability and excluded spawn magnitude. Best-fit variables occurred in eastern PWS and included sea surface temperature, salinity, sea surface temperature variance, and salinity variance from spring to fall. Eight critical life stage periods were defined: 1) adults a year previous to cohort production in late summer, 2) adults a year previous to cohort production in fall, 3) age-0 larval to juvenile herring during late summer, 4) age-0 juvenile herring during fall, 5) age-1 juveniles during spring, 6) age-1 juveniles during late summer, 7) age-2 immature herring during late summer, and 8) age-2 immature herring during fall. There was variation in forcing factor patterns and functional relationships among local PWS regional models. Percentage of total PWS spawn occurring in the eastern region had positive impacts on both southwestern PWS recruitment and on recruit-per-spawner return to PWS while southwestern spawn allocation had negative impacts. Variable in downwelling at the entrance to PWS, freshwater input, and variability in local winds probably affected

zooplankton prey, water column stability, and larval drift differently among PWS regions. These results indicate that spatial complexity is important for population building and support a metapopulation theory with the existence of at least two local populations within PWS. For fishery managers, linear models for PWS recruitment were defined to improve forecasting procedures. For ecosystem modelers, gam results were used to define the critical life stages, areas, variables, and functional relationships for parameterization of a life history-based conceptual model.

Introduction

Pacific herring (*Clupea pallasi*) is an important ecological and commercial species in the North Pacific that responds to long-term decadal climate signals and regime shifts (Ware 1995) and that exhibits extreme variability in recruitment (Zheng 1996). Herring abundance in the northern Gulf of Alaska (GOA), comprised mainly of herring spawning in Prince William Sound (PWS) (Figure 1), is significantly correlated (Chapter 2) to the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and the Aleutian Low Pressure Index (Beamish and Bouillon, 1993). Although the smoothed adult biomass trend for PWS adult herring tracks climate indices (Chapter 2), the un-smoothed spawn magnitude trend (Figure 2a) has sharp peaks that are related to age 3 and 4 recruiting events (Figure 2b and 2c; Funk 1995). This study examines possible causes of extreme recruitment variability leading to short-term "noise" in population trend as opposed to examining effects of climate over smoothed population abundance time series.

Recruit per spawner relationships for herring along the Pacific rim vary from statistically significant to non-existent; model fits are generally worse than for Atlantic herring (*Clupea harengus*) (Zheng 1996). Inclusion of environmental variables improves models. In British Columbia, Canada, significant herring recruitment models exclude spawner magnitude and include sea surface temperature (SST), relative hake (*Merluccius productus*) biomass (an important predator on herring), and an index of El Niño-Southern Oscillation (ENSO) strength (Schweigert 1995). The PWS (Figure 3a), Kodiak Island, and Sitka Sound (Figure 1) herring recruit per spawner relationships are not significant and environmental factors are more deterministic of recruitment in those populations compared to others (Zheng 1996, 1997). The two best Sitlka Sound recruitment models excluded spawners and included SST alone or SST and upwelling (Zebdi and Collie 1995). The addition of environmental variables will likely improve PWS herring recruitment models as well since environmental events coincide with recruitment events; coincidence occurs between recruiting events and the positive anomalies of March freshwater discharge, May-June SST during the cohort year (egg to early larval stage), or average zooplankton standing stock when recruits turn age one (Figure 3b).

Distance between populations with coherent trends provides clues about the scale of physical forcing and the importance of environmental factors to year-class formation. For Pacific herring, a closer coherence is found between recruitment trends in PWS and Sitka Sound than between either of them and other herring stock in the North Pacific and Bering Sea (Zebdi and Collie 1995; Zheng 1996), indicating that similar environmental

factors may affect these two GOA populations (Williams and Quinn 2000a). Based on distances between coherent stocks, Williams and Quinn (2000b) conclude that environmental forcing appears to occur on an oceanographic meso-scale, roughly the size of the eastern GOA (about 400,000 km^2). Monthly SST values from PWS to Puget Sound, Washington cluster into two main groups, occurring at approximately the meso-scale (Zebdi and Colllie 1995). A similar result in distance between coherent stocks is observed for Pacific salmon (Mueter et al. 2002). These results indicate that meso-scale climatic or oceanographic factors, such storm fronts and coastal currents, are important.

Although mechanistic theory exists to explain effects of large-scale environmental factors such as GOA SST and downwelling/upwelling on various herring life stages (Zebdi and Collie 1995; Gargett 1997), concrete evidence of processes in operation is lacking. Large-scale factors provide few clues to indicate time and location of process occurrence. Including smaller scale, life-stage specific local environmental variables may improve recruitment models and help identify time and place of key processes (e.g. Mueter and Peterman 2002). As an example, local winter wind stress prior to hatch of the year class, hake biomass, and annual water temperatures during the first year of life are the three most important factors limiting British Columbia herring year class strength from 1935-1987 (Ware 1995). In another example, warm local SST and low wind driven larval transport are the most important environmental factors affecting Bering Sea herring year-class strength (Wespestad 1991). Differentiation of local stock components may also be possible if the scale of key forcing factors used in analysis is similar or smaller than the scale of spatial stock structure. Indeed, discrete

herring stocks are often defined by their spatial distribution and hydrographic features associated with one or more spawning areas (Cushing 1967; Sinclair 1988). For this analysis, incorporation of local variables provides insight for defining metapopulation structure in PWS (Chapter 1).

While environmental recruitment models for Pacific herring routinely incorporate large-scale environmental factors, this study takes a unique approach with the inclusion of smaller-scale, local environmental factors. Local factors are more likely to be directly involved in processes affecting herring growth and survival than large-scale factors that greatly exceed the effective scale of forcing for local populations. In taking a more focused approach the study objectives are to 1) given the weak recruit-per-spawner relationship for PWS, improve the explanatory power of herring recruitment models by adding environmental factors, 2) improve the environmental recruitment models by accounting for local stock structure and applying appropriate spatial scales to better match environmental forcing scale, 3) examine hypotheses concerning the stock structure theory posed in Chapter 1, 4) identify critical life history periods and key forcing factors on recruitment by using temporally scaled and lagged environmental variables, and 5) review implications and applicability of these results for herring fisheries and ecosystem management.

To accomplish these objectives, a set of biologically meaningful, temporally scaled local and large-scale environmental factors are incorporated into models of recruitment. Models are evaluated by level of significance and model fit criteria. Categorized results are used to identify critical periods in herring life history for year-

class formation. Statistical model comparisons are used to test hypotheses concerning recruitment and stock structure for PWS.

The three null hypotheses tested are:

H_n 1. PWS herring year-class strength is primarily determined by spawner abundance

H_n 2. Distribution of spawn has no effect on R/S ratios.

H_n 3. All geographic units of herring spawning and recruitment within Prince William Sound respond to environmental forcing similarly, i.e. this is single mixed stock or population.

Alternatively, I hypothesize that PWS year-class strength is mainly determined by environmental factors with localized variables being the most important. Furthermore, I hypothesize that factors occurring during the larval and early juvenile stage (age 0-1) will be most important and that spawn distribution affects allocation of recruitment to the different spawning areas in PWS, hereby referred to as local populations (see Figure 1 inset). I hypothesize that metapopulation structure exists as evidenced by variability in local population response to local environmental factors within PWS. Chapter 1 defined metapopulation as a collection of local populations, each with a functionally operational spawning and recruitment unit existing within a spatially explicit geographic region that may or may not overlap with other units. The variability in key forcing factors operating on spatially discrete local populations should therefore manifest as differences in recruitment model parameters and responses among sub-PWS populations.

Methods

Recruitment Modeling

For recruitment modeling, nonparametric generalized additive modeling (gam; Hastie and Tibshirani 1990; Jongman et al. 1995) was used to incorporate environmental variables into stock recruitment analyses (Jacobson and MacCall 1994; Daskalov 1999) because of its flexibility in determining functional relationships. Non-linear relationships can be determined quickly because of the functional smoothers and maximum likelihood algorithms expressed in the model and built into the software (SPlus, version 6.1, 2002, Insightful Corp). Linear models are restricted by the assumptions of normal error distribution, that when violated, can seriously affect hypothesis testing (Spector 1994). In addition, variance often changes with the mean and linear models cannot account for this. Nonlinear data often can be fit to a linear model via transformation and simplify the computations, but it may force the researcher to "interpret the data in unnatural scales" (Hastie and Pregibon 1993). Finally, dependent variables cannot often take on the full range of continuous values that are implied in linear models. Generalized linear models overcome these limitations by reparameterization to induce linearity using the maximum likelihood principle (Chambers and Hastie 1993). The residual deviance (D), deviation from the fitted responses, takes the form -2 $\log_e L$ (L = maximum likelihood) and replaces the residual sum of squares (RSS) in least-square regression (Jongman et al. 1995). The difficulty in using gams for management purposes is that model parameters "flex" when additional values are added to model variables and may therefore change annually. Because linear models are often easier for managers and others to understand,

gam models were compared to the linear forms. The models used in this analysis included a linearized version of the Cushing (1975) model with environmental variables:

$$\ln(R) = a + \sum_{j=0}^{p} B_j E_j + c\ln(S) + \varepsilon \qquad \text{(Hilborn and Walters 1992)} \qquad (1)$$

and a linearized Ricker (1975) model with environmental variables

$$\ln(R/S) = a + \sum_{j=0}^{p} B_j E_j + cS + \varepsilon \qquad \text{(Zebdi and Collie 1995)} \qquad (2)$$

where R = recruitment, E = the environmental independent variable, S = the spawn index, ε = residual error, B = the functional parameter for the relationship of recruitment to the environment, and a and c are the linear scaling parameters. The gam versions of these two models (Jacobson and MacCall 1995) included:

$$\ln(R) = a + f(E) + g(S) + \varepsilon \text{ or } \ln(\frac{R}{S}) = \alpha + f(E) + g(S) + \varepsilon \text{ in the Ricker form} \qquad (3)$$

where the linear parameters B and c are replaced by functions *f(E)* and *g(S)* respectively. In cases where functions *f(E)* and *g(S)* were nonparametric or nonlinear for a variable, I used a polynomial fit to approximate the gam function for the linear model form:

$$\ln(\frac{R}{S}) = a + \sum_{k=0}^{2or3} B_{1k} E_1^k + B_2 E_2 + ...B_j E_j + cS + \varepsilon \qquad (4).$$

For each recruitment variable, I ran single parameter models first then pairs of non-correlated independent variables to see if two-parameter models provided better fits. The restriction in degrees of freedom prevented me from adding more than two variables to any given model. For each single parameter model, I recorded the average Akaike

Information Criteria (AIC; Akaike 1973) which is a measure of model fit. A lower value denotes a better fit:

for gam, $AIC = D + 2p\phi$

and for linear, $AIC = \frac{RSS}{RSE^2} + 2p$.

The residual deviance (D) or RSS is "penalized" by the number of parameters (p). The dispersion parameter (ϕ) approximates variance of the residuals and is therefore equivalent to the linear model residual standard error (RSE) squared. The AIC value provided a quantitative measure of model fit and allowed direct comparison of gam and linear models.

Model Evaluation and Hypothesis Testing

In the model evaluation stage, single parameter models were evaluated in groupings, such as season, region, or lag. Multicolinearity and missing values impaired the ability to construct models with two or more parameters and lowered the degrees of freedom in models. Therefore, evaluation of groups of single parameter models was more practical. Both the total number of significant variables observed and the average AIC score from the gams in each category were used to evaluate models and characterize key environmental factors. With the large number of models and variables, the expectation of spurious relationships is high. This was avoided through a priori selection of variables (Hilborn and Walters 1992), by using only significantly correlated variables with low p-values ($p \leq 0.05$), and by evaluation of model groups rather than individual models. By examining large numbers of significant relationships in a given

comparison, a small number of spurious relationships will not change the overall distribution of model results (Mueter at al. 2002). The p-value represents the probability of expecting a spurious relationship and therefore more weight is given to variables associated with low values (Hilborn and Walters 1992).

After all models were fit, the null hypotheses was tested by comparing the best one and two parameter environmental gam (Eq. 3) or linear (Eqs. 1 and 2) models with models containing only a spawn index parameter using analysis of variance (ANOVA) based on maximum likelihood (Chambers and Hastie 1993). This provided the test for the first hypothesis that year-class strength is primarily determined by the spawner abundance. Models with PWS total and PWS local recruitment that included each of the PWS local spawn index variables, one at a time, were tested for model fit using ANOVAs against each recruitment model using the PWS total spawn index variable. This tested the second hypothesis that distribution of spawn index has no effect on R/S ratios. Finally, the comparison of significant variable patterns and AIC fits for variable categories among the three recruitment and spawn local regions (Figure 1) provided a non-quantitative test of the third hypothesis that all geographic units of recruitment within PWS respond to environmental forcing similarly. Similarly, the alternative hypotheses were assessed by model evaluations of sound-wide versus local variables, a comparison of variables at different lags, and characterization of each of the three recruitment regions by its compliment of significant variables.

Data and Selection of Variables

Pacific herring

For this analysis of Pacific herring recruitment to local populations, two herring variables were created in each of the local regions (Figure 1) in PWS. A spawn index was derived as a measure of spawn magnitude and used as an independent variable in the analysis. Biomass of first-time spawning age- 3 and -4 recruits was used as the dependent variable. PWS herring are often not fully recruited by age 3 (Funk 1995). The proportion and location of the cohort spawning at age-3 may be related to environmental factors affecting early life history stages and be deterministic of cohort size and location by age 4. Because age-4 is the youngest age included in age-structure-analysis (asa) for forecasting (Funk 1995), quantifying the relationship between age-3 and -4 recruits may improve predictions of initial year-class size for the asa management model. For these reasons, the abundance and distribution of age-3 recruits were important to include in the recruitment analysis. Initially, a spawn index and age-3 and –4 recruitment biomass variables were created in each of five spawning regions (Figure 1; Table 1). The spawn index and biomass of recruits were derived from three types of information collected for the purpose of fishery management since 1973 by the Alaska Department of Fish and Game (ADFG) (Brady et al. 1987; Biggs et al. 1992; S. Moffit and J. Wilcock, personal communications and unpublished data, ADFG, P.O. Box 669, Cordova, Alaska 99574). Lineal beach coverage of spawn, the first data type analyzed, is easily observed from the air as white patches in the water and was recorded daily by ADFG during the spawning period. The cumulative daily spawn coverage, reported as "mile-days" by region (Figure 2a), represented the annual spawn index. For each cohort year, spawn mile-days were totaled for each local region (Figure 2a) and for PWS as a whole. Because mile-days

reflect the number of days a site receives spawn (Brady et al. 1987; Willette et al. 1998), the spawn index was a proxy measure for spawner- or egg-density and therefore useful in testing population density-dependent effects. The aerial spawner index represented escapement from the fishery and was therefore independent of fishery removals. The second type of ADFG data used, the peak adult spawning biomass, was defined as the largest observed sum of estimated individual school biomass as observed from the air occurring over the range of spawn dates in a given geographic area. The third data type was age composition and age-specific proportion, derived from net sampling, of the PWS adult spawning biomass for each of the five local regions. Age, weights, and lengths were measured from one or more large samples (> 600 each) of herring at each local region. To create the recruitment variables, the age-3 and -4 proportions of biomass were multiplied by the peak adult spawning biomass for each local region and for PWS as a whole to obtain regional-specific and PWS total age-3 and –4 recruitment by weight. Finally, a PWS recruit per spawner (R/S) variable was created for age-3 and –4 by dividing the PWS recruitment biomass over the PWS total spawn index.

Environmental

Environmental factors were selected based on their inclusion and significance in previous herring recruitment analyses (Schweigert 1995, 1996; Zebdi and Collie 1995; Daskalov 1999; Williams et al. 2000b; Fiksen and Slotte 2002) and known impacts on ocean productivity that affect zooplankton food resources for herring early life history stages (Legendre 1981; Ware 1995; Gargett 1997; MacFarlane et al. 2000). Variables representing climate were chosen based on the known correlation between herring

population and climate trends (Chapter 2). Freshwater discharge was chosen because of its known effect on stratification (Royer 1982) that in turn affects coastal ocean productivity. Upwelling or downwelling is an indirect indicator of climate and affects the transport of GOA water and zooplankton into PWS (Cooney et al. 2001). Winds and the Alaska gyre in the GOA cause mainly downwelling outside the entrance to PWS except during June through August (Bakun index; Bakun 1973, 1975). The strongest downwelling occurs during December through February. Winds affect egg removal rates, horizontal transport and vertical mixing of the upper surface potentially affecting herring egg survival, larval transport, and zooplankton production (Chapter 1). Temperature directly affects growth (Chapter 1). Salinity, temperature, and the variability of each may also be proxies for stratification, the mixed-layer depth, and other processes affecting larval transport, food availability and herring growth (Chapter 1). The selection of factors affecting the upper 20 m was based on known and hypothesized geographic distribution of PWS spawn and herring early life history stages (Brady et al. 1987; Biggs et al. 1992; Norcross et. al. 2001). Although variables representing predation are included in previous analyses (Schweigert 1995; Ware 1995), they were not included here due to lack of data on PWS herring predators. The only top down process represented was removals by the fishery. Because the spawn magnitude index used was independent of fishery removals, including both in a model did not violate assumptions of independence. Fishing catches were obtained from ADFG (J. Wilcock and F. Funk, personal communications and unpublished data, ADFG, P.O. Box 699, Cordova, Alaska 99574).

All environmental variables were lagged to identify the life-stage affected. These included: –1, representing the year prior to the cohort year and affects on adults; 0, the cohort year encompassing pre-spawning adults from January to April, embyros from April to early May, larvae from May to late summer, and early age-0 juvenile stage through December; 1 representing age-0s from January to April and age-1 juveniles thereafter; and 2 representing age-1 until April and age-2 thereafter including the period in late summer when age-2 join the adult population (Chapter 1).

To evaluate environmental effects on recruitment by spatial scale, environmental variables were categorized into two spatial forcing categories. Sound-wide variables were large-scale factors with a single value representing environmental forcing over large regions (≥ PWS) over a given temporal period. These were further categorized as North Pacific, Northern GOA, and PWS representing the area over which forcing was applied (Table 1). PWS local variables were small-scale local factors representing forcing over areas within PWS (Table 1; Figure 4). For each variable, an anomaly was estimated from the mean value over the time period of available data described below.

Types of environmental variables used fell into the general categories of 1) climate, 2) freshwater discharge, 3) upwelling or downwelling, 4) wind, 5) precipitation, and 6) air temperature, 7) zooplankton production and 8) PWS hydrography, and 9) fishing mortality (Table 1). Climate indices included the monthly Pacific Decadal Oscillation (PDO) based on North Pacific monthly SST anomalies and the monthly ENSO index based on SST anomalies in a bounded region in the Pacific Ocean. Also included was the monthly Pacific Inter-Decadal Oscillation (PIDO) and the Pacific

Multi-Decadal Oscillation (PMDO) based on the residuals of the ENSO fit or "non-ENSO" SST signal. Finally, I used the annual Aleutian Low Pressure Index (ALPI) based on winter North Pacific sea surface pressure anomalies over a fixed region and the annual Atmospheric Forcing Index (AFI), which represents a combination of the ALPI, the winter PDO and a winter atmospheric circulation index (Table 1). Positive AFI values represent intense Aleutian lows, above average frequency of westerly and southwesterly winds, cooling of sea surface temperatures in the central North Pacific, and warming within North American coastal waters (MacFarlane et al. 2000). All these indices were obtained directly from the authors cited in Table 1.

Monthly freshwater discharge was an index developed by Royer (1982) for the entire eastern GOA region based on precipitation, drainage area topography, and air temperatures affecting snow and ice melt. This index was obtained from the University of Alaska, Institute of Marine Science database.

The monthly Bakun Upwelling index (Bakun 1973, 1975) for Hinchinbrook Entrance (Figure 4, ENT), the eastern opening of PWS to the GOA, was obtained from the National Atmospheric and Oceanic Administration (NOAA). Because Hinchinbrook Entrance is mainly a downwelling system, positive anomalies represent a relaxation in downwelling during spring, fall and winter and intensified upwelling during the summer.

A suite of wind, precipitation and air temperatures variables was derived from meteorological data available for the Northern GOA and PWS. Hourly values of wind speed (knots), precipitation and air temperature were obtained from the National Climate

Data Center (NCDC). Mean monthly values were calculated for each series. The only site nearby PWS with a long time series of wind data available was Middleton Island, about 50 km south of PWS in the Northern GOA (Table 1). Energy required to induce vertical mixing, profoundly affecting ocean productivity, is related to the third power of wind speed (Mann and Lazier 1991). Therefore, a proxy for mixing was estimated as the cube of mean wind (MW^3). Because variability in wind and the frequency of storm events may be more deterministic of oceanic production than mean values in a given time period, three additional variables were created. The variance of the mean wind speed (VW) was estimated along with two "wind event" variables. The first was estimated as the number of times per month wind speed exceeded 25 knots (labeled high speed events or HSE). The second as the number of times per month it exceeded 35 knots (labeled gale force events or GFE). Both HSE and GFE were normalized for the total number of observations made in a given month. Within PWS, the Cordova airport (eastern PWS) had the longest historical time series of air temperature and precipitation and therefore monthly values were estimated from that site.

The longest time series of zooplankton data available was from a single site, the Armin Koernig Hatchery on Evans Island in southwestern PWS starting in 1981. Daily zooplankton settled volumes (ml/m^3) were generally collected over a four-month period from mid-March to mid-July in PWS operated by the Prince William Sound Aquaculture Corporation (Cordova, Alaska) for the purposes of determining hatchery salmon release dates. Two annual zooplankton variables were created from this dataset. A mean density was estimated over a six-week period, April through mid-May, when missing data points

for each year were minimal. A peak density was calculated as the highest zooplankton density sampled during that same six-week period.

The PWS hydrographic variables were calculated for seven local regions (Figure 4) delineated using observed and modeled oceanography for PWS. The data categorized into the seven regions came from a large historic database of hydrographic information for the GOA and PWS residing in the University of Alaska, Institute of Marine Science database. Niebauer et al.(1994) describe the circulation in PWS to include 1) an inflow region (Entrance or ENT in Figure 4), 2) an central gyre present at times (Central Sound or CS in Figure 4), 3) two outflow regions (Southwest or SW and Montague Strait or MS in Figure 4), 4) two northern fjord areas heavily influenced by freshwater flow (North Shore or NS and Northeast or NE in Figure 4), and 5) an eastern shelf region influenced by the GOA by transport of gulf water through the entrance (Southeast or SE in Figure 4). This circulation is mediated by seasonal and interannual variability in winds, freshwater flow, and strong cyclonic winds over the GOA that induces coastal downwelling and strong flow into PWS. The seasonal circulation pattern was modeled using freshwater runoff, surface heat flux, the Alaska Coastal Current (ACC) throughflow in PWS, daily spatial varying wind speeds, and the tides, which are large in PWS (up to 8 m) (Wang et al. 1997, 2001). As an example, the composite SST (1972 to 1999) and residual model for May, when PWS herring hatch and begin larval drift, is shown in Figure 4. Although there were significant ($P < 0.05$) correlations among the PWS regional hydrographic data sets, the relationships were not consistent among months for data set pairs. Therefore, all seven PWS oceanographic localities were

retained in the analysis. Because variability of ocean conditions may be more influential to survival than mean conditions, the monthly variance for each mean SST and sea surface salinity (SSS) value was also estimated.

Over 1000 variables were created including the lagged forms (Table 1). This included 4 spawn variables, 10 recruitment variables, and 1,033 environmental variables comprising 473 sound-wide forcing factors and 560 local PWS forcing factors.

Data Transformations and Reduction of Variables

The distributions and scale of variables were adjusted. The dependent recruitment variables were log transformed to correct skewing. The effect of varying scale within the environmental variables was corrected by normalization and applied as anomalies from the long-term means calculated over the time periods listed (Table 1). Spawn variables were applied as untransformed and log-transformed.

Exploratory analysis led to an understanding of interactions between variables and to reduction of them. Scatterplot matrices were used for simultaneous exploration of multiple variables. Variables with potential interactions, whether linear or non-linear, were examined further. Time series techniques (Diggle 1990) were used to determine significant cross-correlation and multicollinearity among variables while accounting for temporal autocorrelation. Monthly series with the highest ($r > 0.70$), significant ($P < 0.05$) cross-correlation coefficient were pooled in order to reduce the number of variables. The PDO, PIDO, and PMDO (Table 1) values were highly correlated ($r \geq 0.80$, $P \leq 0.001$) among all months with even higher correlation ($r \geq 0.90$) among three-month intervals representing four seasonal periods (e.g. December– February., March –

May, etc.). Each climate index was therefore pooled within seasons. Monthly upwelling indices were uncorrelated and retained as monthly values. Monthly fresh water discharge series were significantly correlated ($P \leq 0.001$) only between December and January, January and February, and February and March but with a relatively low correlation coefficient ($r \leq 0.67$); this series was not pooled among months. For wind variables, correlation coefficients between monthly pairs through June (e.g. January and February, March and April) were relatively high ($r \geq 0.70$, $P \leq 0.04$) and were pooled in two-month periods. July wind values were left out of the analysis as most values were near zero. August wind values were not correlated with any other month. September through November wind values were pooled ($r \geq 0.70$, $P \leq 0.04$) and December values were uncorrelated with other months (Table 1). For the PWS salinity and SST data, correlation matrices were used to reduce variables, in addition to time series and scatterplot matrices, due to the large numbers of missing values. There were significant ($r \geq 0.70$, $P < 0.05$) correlations between consecutive months and therefore PWS local variables were combined in two-month periods starting with January-February and ending with November-December. Although SSS and SST were correlated between some pairs of regions in a given bi-monthly period, the correlations were not consistent for all time periods. For example, during the winter, SST in four of the seven localities were correlated, but during the summer SST was significantly different from one another in the same four. Therefore, no adjustments were made for inter-locality correlations.

For the herring recruitment variables, recruiting regions were combined if they were significantly correlated for both age 3 and age 4 recruits. As a result, the southeast and northeast areas were pooled ($r= 0.978$, $p=0.0001$ for age 3; $r=0.743$, $p=0.001$ for age 4) as well as the North Shore and Naked Island areas ($r=0.675$, $p=0.01$ for age 3; $r=0.804$, $p= 0.005$). The variables created were the Eastern (E3 and E4; Table 1) and the Northern (N3 and N4) resulting in a total of five response variables for each age (E, N, MT, TOT, R/S; Table 1). The same type of pooling was applied to the spawn regions resulting in four spawn index variables (ESPN, NSPN, MTSPN, TOTSPN; Table 1). The Eastern, Northern, and Montague variables represented the three hypothetical local populations composing the PWS metapopulation (Chapter 1).

Tests for Independence and Variable Grouping

Prior to the addition of an environmental variable, the recruitment and spawn relationship was examined by time series analysis and via a correlation matrix. All herring recruitment variables were log-transformed to correct skewed distributions. The spawn indices were distributed relatively normally, however, there was a large scaling difference between spawn and recruitment values. Therefore, the spawn index was tested log-transformed and untransformed to address the scaling issue.

Environmental variables were evaluated for inclusion in recruitment models using correlation analysis to determine level of significance to recruitment and independence among variables. If a large proportion of correlated variables were found, identification of important environmental effects on recruitment would be difficult. To be valid, a model assumes independence among variables. Tests for independence was

done to prevent inclusion of related variables in the same model. The environmental variables were cross-correlated with each dependent variable using time series analysis and a significance level of 0.1. Secondly, significantly correlated variables, including lags from –1 to +2, were identified (see Appendix I for list of all significant variables) in a correlation matrix with each recruitment variable. The degree of interaction among variables impacted the interpretation of variables; variables with high levels of interactions were interpreted as a variable family. For modeling, variables were tested one at a time for significance level and the best-fit variable, from a group of related variables, was selected as the representative for that group. From this evaluation, a list of significant environmental factors, the r and p values were compiled for each response variable (Table 2).

Correlated groupings of variables, especially within a given parameter type such as wind or upwelling, often spanned several lags. In those cases, Principal Components (PC) analysis (Mardia et al. 1979) was used to further reduce variables (see Appendix II for PC definitions). New variables were created using only the PCs that accounted for over 90% of the variation within a variable grouping. The new variables consisted of linear combinations of the original variables using the loadings for each PC as coefficients. These PC variables were tested for improved model fits over the individual variables represented in each PC.

Results

Environmental Recruitment Modeling

A total of 705 of the 9970 possible environmental and fishing mortality variables, were significantly correlated to recruitment variables collectively (Table 2), there was some redundancy in the use of variables among models, and local variables were more highly represented. The total significant variables represented 7.1% of the total possible and out of those, 316 were unique. Redundancy (significance with more than one recruitment variable) was particularly high for zooplankton, followed by high speed wind events, variance in SST, upwelling, and variance in salinity (bolded values in Table 2; redundancy rate = total number of variables in a given category included in models / number of unique variables in that set). By scale of environmental forcing, 4.9% (88 unique) were soundwide and 8.7% (228 unique) represented local within PWS. For comparison, 19.9% of the total possible unique soundwide (88 out of 442) versus 40.6% (228 out of 562) for local variables were significant in models.

Among recruitment variables, there were differences in numbers of significant variables, types of variables, and model fits according to AIC with lower scores denoting better model fit (Table 2; Figure 5). The total number of significant variables for each recruitment variable ranged from a low of 65 for PWS total age-4 recruitment a high of 91 for Montague age 3 (Table 2). Except for the Northern area, age-3 recruitment was correlated to more environmental variables than age 4 (Appendix I). There were generally more PWS local variables correlated to recruitment. The ratio of local-to-sound-wide variables was lower for the Eastern and Northern recruitment

regions and for the PWS R/S age-4 recruitment than for others. Model fits were universally better for local environmental variables. Compared to the other responses, Eastern age-3 models had relatively poorer fits with both sound-wide and local environmental variables while Northern age-3 and age-4 models had relatively poor fits only with sound-wide variables. Fishery mortality appeared to have no effect on recruitment. Fishery catches were not significantly correlated to any of the recruitment variables, whether log transformed or not. The scatterplot matrices failed to reveal any apparent non-linear relationships. Therefore, the fishery removals were not included in any of the models.

The addition of environmental variables significantly improved the explanatory power of both age-3 and age-4 recruitment models and the gam smoothing functions revealed functional relationships with the environmental variables. For age-3 recruit per spawner models, PWS total spawn index was significantly correlated only at the 10% level and only with a non-linear fit; the lm was better than the gam (Table 3, models 1 and 2). The addition of SSS to the model significantly improved the fit over the single parameter spawn index model (ANOVA, $p = 0.03$ for gam models 3 versus 1 and $p < 0.01$ for lm models 4 versus 2 and 5 versus 2). In this case, the gam model (Table 3, model 3; Figure 6a) had the best fit according to the R^2 and AIC values. The smoothing functions show the weak negative relationship with PWS spawn index (Figure 6b) and the weak negative correlation to the lagged summer salinity (Figure 6c). The lm (4) provided almost as good a fit and had significant regression coefficients. Other models containing only environmental variables (Table 3, models 6-11) performed better than

models containing only a spawn index variable (Table 3, models 1-2). According to residual deviance, R^2, and model AIC, the two best models of age-3 recruit-per-spawner ratios were gam fits of zooplankton and SSS (Table 3, model 6; Figure 7a) and a principal component variable of wind and SSS (model 9), both explaining over 90% of recruitment variation. The failure of gam models to achieve significant regression coefficients was probably due to the low sample size. However the smoothing functions reveal the positive relationship of zooplankton (Figure 7b) and the negative impact of lagged summer salinity (Figure 7c). The lm versions (Table 3, model 8 and model 11) were nearly as good as the gams, explaining over 80% of recruitment variation and included significant regression coefficients. All 2-parameter environmental models (6-11) provided significantly better fits (ANOVA, $p \leq 0.004$) than spawn index alone (1 and 2). The ANOVA results led to a rejection of H_n1 (year class dependent on spawn index) for age-3 recruits.

The results for age-4 recruit per spawner model differed from age-3 models by environmental models with lower explanatory power and by effects of spawn distribution on recruitment (next section; e.g. Figure 8a). The inclusion of environmental variables (Table 4, models 6-12) improved model fits significantly over those with spawn index parameters (ANOVA, $p \leq 0.01$) leading to a rejection of H_n1 (year class dependent on spawn index) for age 4 recruits. However, the addition of environmental variables did not improve recruitment models to the degree observed for age-3 models as the AIC values for age-4 environmental models were generally higher than for age-3. The two best age-4 models were gams containing Eastern age-3

recruitment and PWS September-October salinity, -1 lag (Table 4, model 6, Figure 9a) or containing zooplankton, +1 lag, and mean wind speed in January-February, 0 lag (Table 4, model 10, Figure 10a). The smoothing function fit with Eastern recruitment improved (Figure 9b) over the previous model (Figure 8b) with the addition of fall salinity that has a dome-shaped relationship to recruitment (Figure 9c). The positive relationships to zooplankton and winter winds are also shown (Figure 10b and c). The lm versions (Table 4, models 8 and 12) were also significant and explained over 70% of the variability in recruitment.

Local Stock Structure

Significant interactions among spawn and recruitment variables indicated that the three local spawn regions were independent and that localized Eastern area recruitment was more deterministic of overall PWS recruitment than other recruitment variables (Table 5). Both the untransformed and log-transformed versions were examined to increase the detection power of significant correlations since the distributions of data were slightly skewed in some variables. All local spawn indices (Figure 1) were positively correlated with PWS total spawn index but none were correlated with each other, indicating independence among the three spawning local regions. Among age-3 recruitment variables, all local variables were correlated with the PWS total age-3 recruitment with the strongest degree of determination from Eastern age-3 and the weakest from Northern age-3 recruitment. Among local regions, only Eastern and Northern area age-3 were correlated and that occurred at a low level ($r = 0.5$). Similar to age-3 recruitment, all three local age-4 recruitment variables were

correlated with PWS total recruitment, however, the highest correlation occurred with Montague age-4 as well as Eastern age-4. All three local age-4 variables were also correlated to PWS recruit-per-spawner (R/S) production, but with Eastern age-4 the highest. Different from age-3, age-4 local regions were significantly correlated with one another but only the Northern and Montague age-4 recruitment occurred at a higher level ($r > 0.5$). Because only a proportion of age-3 herring spawn in a given year, the interactions between age-3 and age-4 recruiting variables indicated the level of regional dependence of recruitment success at age 4. The highest correlations occurred between age-3 and age-4 within localized regions with the highest overall in the Eastern region. Only Eastern age-3 recruitment had correlations to PWS total recruitment or the recruit-per-spawner (R/S) production at a higher level ($r > 0.5$) as demonstrated earlier in the age-4 recruitment models (Table 4, models 3-9; Figure 8b). Eastern age-3 and –4 recruitment appeared to be consistently more deterministic of total recruitment in PWS than the other two regions.

These results were probably the strongest evidence of the relative importance of Eastern recruitment to the PWS population as a whole.

Distribution of spawn was important because recruitment was significantly correlated to spawn magnitude only at local scales, only the Montague recruitment region showed a dependence on spawning, and only Eastern spawning produced positive correlations with other regions (Table 6). For age-3 recruitment, only the Montague region showed a dependence on spawning, spawning in the north had negative impacts, and spawning in the east had positive impacts. For age-4, eastern spawning had positive

impacts on Montague and PWS total recruitment while Montague and northern area spawning had negative impacts. Therefore, distribution of spawn appears to impacts recruitment and recruit-per-spawner production in PWS.

The formal test of H_n2 (distribution of spawn index has no effect) was in the comparison of model fits. For age-3, H_n2 could not be rejected because regional spawn index variables provided worse or non-significant model fits as compared to PWS total spawn index (Table 3, models 1 and 2). However, for age-4 recruitment, the best one-parameter models with spawn index included non-linear fits of Montague area spawn index (Table 4, models 1 and 2). The model fits with either Northern or Montague spawn index were significantly better (ANOVA, $p < 0.0002$) than model with PWS total spawn index. Note that the coefficient for the lm was negative, indicating a negative impact of Montague spawn index on recruitment as found in the linear correlations (Table 6). The smoothing function plot illustrated this negative relationship of recruitment to Montague spawning (Figure 8c). These comparisons led to a rejection of H_n2 for age-4 recruit-per-spawner ratios and conclude that distribution of spawn index appears to have a stronger impact on recruitment than total PWS total spawn.

Differences in localized environmental forcing among recruitment regions were evident in patterns of significant environmental variables compared by number, AIC, sign of functional response, and shape of functional response.

Variation in the numbers of significant environmental variables and model fit (AIC) among recruitment variables indicated that the type of environmental forcing is unique to each recruiting region (Table 2, Figure 11, 12, and 13). The proportion of

significant variables from each of the local hydrographic regions was different among the three recruiting regions but similar between Eastern and PWS R/S for both ages and between Montague and PWS total recruitment for both ages (Figure 11). Eastern and PWS R/S recruitment were correlated to Northern GOA variables to a greater degree than Montague and Northern recruitment (Figure 11). North Pacific forcing variables were most important to Northern recruitment models. Patterns in the variable type and AIC, for that type, were also different among recruitment regions (Table 2, Figures 12 and 13). Although large numbers of local hydrographic variables were important, the AIC values were much lower for Montague age-3 and total age-3 recruitment than for Eastern age-3 recruitment (Figure 12). For Eastern age-3, the best fitting variables were zooplankton, mean wind speed, and variance in wind speed (Table 2, Figure 12). In contrast, Montague age-3 was not correlated with zooplankton (Table 2, Figure 12). For age-4 models (Table 2, Figure 13), large numbers of local environmental variables were significant, the AIC values were generally lower for the Eastern region and the PWS total recruitment, and zooplankton was excluded only from Montague models.

Variation in functional response, as the number of positive versus negative correlations of environmental to recruitment variables, provided more evidence for differences in regional forcing among recruiting regions. Categorized by scale of forcing (Figure 14a), the patterns were different among recruiting regions, especially visible for age-3 variables. An example is Southeast (SE) PWS variables important for Montague age-3, but not Eastern age-3. Another is North Pacific variables with positive and negative effects on Eastern age-3, mainly negative on Northern, and no impact on

Montague recruitment. Categorized by type of variable (Figure 14b, Appendix III), differences among recruitment regions were evident by examining the wind variables (MW, VW, MW3, and WE), the upwelling index (UW), and zooplankton (Z).

Finally, region-specific differences were evident by comparing the shape of functional responses, derived from the smoothing functions used to fit the gams recruitment models. An example was the response to zooplankton + 1 lag that was positive in the East and North, but mostly neutral at Montague (Figure 15). Anomalously high December upwelling, prior to the cohort year, had a negative effect in the East and North that was not apparent at Montague (Figure 16). In addition, the response to local variables was region specific. Eastern age-3 recruitment was more strongly correlated to fall salinity in East than to values in southern PWS (Figure 17a and b). The opposite was true for Montague with a tighter correlation to fall salinity in the closest region of PWS (Figure 17c and d).

The qualitative comparison of the significant variables and AIC values for Eastern, Northern, and Montague recruitment (Table 2; Figures 11, 12, 13, 14,and 15-17) led to a rejection of H_n3 (geographic units of recruitment respond similar to environmental forcing) and a conclusion that metapopulation theory is appropriate for the herring in PWS. There was variation in forcing factor patterns and functional relationships within models by regions within PWS. Eastern and northern recruitment were more heavily dependent on zooplankton production, upwelling and freshwater flow than southwestern (Montague) recruitment. Percentage of total PWS spawn occurring in the Eastern region and age-3 recruits had positive impacts on both southwestern PWS

recruitment and on recruit-per-spawner return to PWS while southwestern spawn allocation had negative impacts. Models were improved by accounting for local stock structure and applying an appropriate, localized spatial scale over monthly or seasonal temporal periods for the environmental forcing factors. These factors led to a conclusion that there are localized populations within PWS and that metapopulation theory is more appropriate than assuming PWS is composed of a single population.

Critical Life History Periods

Allocation of best-fit variables by season or lag differed among recruitment variables, spring (March-April) through fall (September-November) was included, and late summer (July-August) variables had the best overall model fits (Table 7). Virtually all the unique significant variables (704 out of 705, excluding fishing mortality) represented seasonal periods (Table 2; Figure 18a). Winter (December-February) had the smallest proportion of significant correlations to recruitment (Figure 18a) and worst average model fit (Table 7). Late summer had the best average model fit. Allocation of lagged variables was different across recruitment indices (Figure 18b) and the +2 lag had the smallest proportion of significant variables and worst average model fit (Table 2). The +1 and -1 lags had the highest proportions of significant variables, and the +1 lag had the best average model fit as well as the highest redundancy rate (Table 2). For most recruitment regions, there were several best fitting (AIC < 10.0; bolded and highlighted in Table 7) season and lag combinations. Only Eastern age-3 recruitment had no AIC values below 10.0 with the best fitting variables during the +1 lag for spring. Age-4 models had more best fitting combinations (23 total) than age-3 (12 total) with the

highest number for PWS total recruitment and PWS recruit per spawner production (8 each) while Eastern age-4 had the highest number (4) among local recruitment variables (Table 7). Late summer (17) had more best fitting values than fall (7), spring (6) or early summer (5). The –1 (13) and +1 (11) lags had more best fitting values than +2 (6) and 0 (5) lags. The combination of late summer and -1 or +1 lag produced low AIC values (< 10.0) for 6 out of the 10 recruitment variables and had the lowest overall average AIC values across recruitment variables (12.59 and 8.86) (Table 7).

Examining only spring through fall variables, the key environmental forcing regions were northeast and southeast PWS for all recruitment variables except Eastern age-3 (Table 8). Low (< 10.0, bolded and highlighted) AIC values were obtained only with variables representing local forcing within PWS at the Entrance (3 low values), Montague Strait (3), Northeast (9), the North Shore (5), and Southeast (7). The lowest average AIC values occurred at the Entrance (13.42) and Southeast (13.51). The highest proportion of significant variables was in the Northeast, North Shore and Southeast (all over 12%). For Eastern age-3, the only recruitment variable without a low AIC value for Northeast forcing, the best average model fit occurred at the Entrance to PWS.

The key environmental variables were salinity, sea surface temperature (SST), the variance of the two, and zooplankton for spring through fall variables (Table 9). Except for Eastern age-3 recruitment, the lowest AIC values (bolded in Table 9) occurred in the four oceanographic variables representing salinity and SST. Zooplankton had the lowest AIC for Eastern age-3 recruitment and the highest proportion of significant variable (21.3%) for all recruitment variables combined. Variance in salinity

(4) had the most best fitting AIC values (< 10.0, bolded and highlighted in Table 9), followed by salinity (3), variance in SST (2), and SST (1). Salinity and SST had the lowest categorical average AIC values (bolded in Table 9). The majority of these oceanographic variables occurred in local regions within PWS. Unfortunately, zooplankton represented a soundwide forcing variable and could not be examined on a local scale.

Eight potentially critical life history periods were defined from the important combinations of season, lag, location, type of variable, and sign of functional response Table 10). The results underscored the importance of physical forcing in Northeastern and Southeastern PWS. By examining only combinations that produced a low AIC value (highlighted in Table 10) for one or more recruitment variables, included were spring, late summer and fall, different combinations of lags for each season, the Northeast and Southeast local regions, and all local oceanographic variables. This resulted in defining eight critical periods. The spring +1 lag period coincided with the end of the first juvenile herring overwintering period, first birthday, and the major zooplankton bloom in PWS. The key variable in spring was salinity with a positive relationship to recruitment. Late summer -1 lag coincided with adult rearing and feeding prior to the cohort year. During this period, recruitment responses to increasing SST values were positive while responses to variance in salinity and variance in SST were negative. Late summer 0 lag coincided with the age 0 late larval stage, metamorphosis, and entry into the juvenile nursery areas. Recruitment responses to SST were variable, positive for Eastern age-3 and PWS total age-3 and negative for Montague age-3. Late summer + 1

lag coincided with juvenile feeding and rearing within the nursery areas prior to overwintering. Recruitment responses to salinity were positive and to SST, negative. Late summer +2 lag coincided with the exit of juveniles from the nursery bays and the joining with adult schools for the first time; the response to variance in SST was negative. The fall -1 lag coincided with the beginning of the adult overwintering period prior to the cohort year with negative recruitment responses to increasing variance in salinity and variance in SST except for Northern age-3 where the response to variance in SST was positive. The fall 0 lag coincided with the beginning of the first overwintering period for juveniles within the nursery areas with a positive response to salinity only for Montague age-3 and negative response for all others. Finally, the fall +2 lag coincided with the beginning of the first overwintering period for juveniles outside the nurseries areas and joined with adult schools. The single recruitment response was positive for salinity. Of all the categories over all recruitment variables, the 23 lowest AIC values occurred in the Northeast 19 times, late summer 12 times, fall 9 times, and the –1 lag 14 times. Clearly, oceanic conditions in the Northeast, during the adult rearing and overwintering period prior to producing the cohort, are critical to year class strength.

Examining the suite of significant variables within each of the eight critical life history periods provided clues as to key processes potentially affecting recruitment (Table 11, Figure 19). Life history information from Chapter 1 was used to further define the geographic boundaries of forcing. For spring +1 lag, positively correlated zooplankton, winds and upwelling were included with forcing expanded to the PWS Entrance and the North Shore. These indicated the potential importance of stratification,

the bloom, and influence on the two from the Gulf of Alaska at a time when age-1 juveniles are broadly distributed in the nearshore within PWS bays. For late summer –1 lag, the suite included most regions of PWS with positive affects from SST and negative affects from salinity and variance in salinity and SST. These indicated the importance of stratification and temperature for feeding and growth of broadly distributed adults a year prior to spawning. For late summer 0 lag, winds were included with forcing across much of PWS and responses similar to the –1 lag for late summer. For broadly distributed age-0 herring close to metamorphosis, stratification and temperature, along with wind-driven transport, may be important for growth and arriving at nursery sites. For late summer +1 lag, responses to salinity, SST, and variance of the two were opposite that for late summer 0 or –1 lags and two recruitment regions were unaffected during this period. The same factors that may improve growth and feeding for age-0 entering bays and adults outside of bays may have negative affects on food resources in some of the nearshore zones within the bays where the age-1 herring reside. During late summer +2 lag, 6 of the 10 recruitment variables were correlated to variables and the key forcing regions were in the east. The negative response to variance in salinity and SST may indicate that in some areas, mixing may have negative impacts on recruitment at a time when juveniles are leaving the nursery areas to join adult schools. For fall –1 lag, freshwater flow, winds, and the entrance and exits to PWS as well as the North Shore were included with positive responses salinity and geographically variable responses to variance in salinity and SST. These indicate that wind mixing may be important in keeping salinity values high in the upper waters providing favorable conditions for

overwintering adult herring the year prior to spawning. For fall 0 lag, upwelling and winds were included as well as the entrance and exits to PWS and the North Shore with negative responses to salinity, SST, and variance of the two. For age-0 herring entering their first overwintering period in bays, excessive mixing may have negative impacts on feeding and growth, opposite to the response observed in the adults during the fall. For the fall +2 lag, 6 of the 10 recruitment variables were correlated to variables from regions similar to the other two fall periods. During this period, immature herring are overwintering with adult herring (fall –1 lag) but differences in response and key variables were observed between the two periods. Mixing and ocean conditions may affect feeding and survival differently for immature versus adult herring mixed together at the same locations. These results (Table 11, Figure 19) were important as they facilitated formulation of specific recommendations for monitoring needed to improve fisheries management models and to parameterize ecosystem-based models (e.g. the conceptual model presented in Chapter 1).

Discussion

Environmental Recruitment Models

The inclusion of local environmental variables in generalized additive models (gams) notably improved explanatory power of herring recruitment models. Environmental forcing, especially on a scale smaller than PWS, was more deterministic of PWS recruitment than total spawn magnitude. The combination of incorporating local environmental factors and using flexible gams resulted in models explaining up to 91% of the variance in PWS herring recruitment. The best-fit recruit per spawner models

produced by Zebdi and Collie (1995) also included environmental parameters and explained about 70% of the variability in recruitment of Sitka Sound herring, a population coherent with PWS in recruitment and weight-at-age trends (Zheng 1996; Williams and Quinn 2000a). However, they used SST and upwelling indices that represented a much larger area than encompassing the local population. Upwelling was also significant in the models shown here, but model fits were higher with oceanographic variables, such as SST and salinity at scales smaller than PWS. The results presented here were more comparable to gam model-fits achieved for sprat and anchovy recruitment (Daskalov 1999). For sprat, a model of recruitment to spawn explained only 35 % of the variability, comparable to this study with 34% for age-3 and 38% for age-4 herring. With the addition of principal component factors, representing a co-varying set of wind conditions and a similar set for freshwater inflow and SST, model fits were improved to 75% (Daskalov 1999). Anchovy had a much stronger initial recruit to spawn relationship at 72%, but again was improved to 92% with the addition of a wind and a river discharge variable. Wind and SSS, a factor heavily influenced by local freshwater input, were also key variables in the analysis presented here.

Local Stock Structure

The results of this study led to the rejection of hypotheses that distribution of the spawn has no effect on recruitment and that PWS comprises a single mixed stock. Population building may be lower or non-existent in PWS without a healthy Eastern population. This Eastern influence may be due to the dependence of the local Montague population on migrants for maintenance and to the higher survival of recruits in the East.

In Chapter 1, the Montague region was theorized to be heavily dependent on migrants from Eastern and Northern local populations with loss of spawning in the East negatively impacting the population. Evidence for the existence of local populations was theorized to occur as differences in local environmental forcing. The results of the study support both theories. A strong dependence of age-4 recruitment in all areas on Eastern age-3 recruits was observed. The influence from Northern age-3 recruits was weaker and Montague age-3 recruitment benefited only the Montague region. The best recruitment model fits included environmental variables from the East (Northeastern and Southeastern local regions). In a recent study of PWS juvenile herring nursery areas, modeled overwinter survival rates from a single year ranged from 7 to 91% in the Montague region and 64 to 99% in the Eastern region (Norcross and Brown 2001). Over a three-year period, an Eastern bay had consistently higher juvenile densities than a Northern and a Montague area bay despite the small adult population in the East compared to Montague during those years (Norcross and Brown 2001). If PWS were a single large mixed population, regional allocation of spawn should not have an observable impact on recruitment to PWS as a whole. However, the regional spawn index did have an affect with Montague spawn index negatively impacting and Eastern spawn index positively impacting recruit-per-spawner production. The correlation between the declining proportion of Eastern spawn index and downward trend in recruit-per-spawner production was demonstrated in Chapter two. A shift in spawn allocation, away from the East, would therefore cause lowered recruitment to all of PWS. The evidence for spatial structure was in the observed variation in patterns of regional

recruitment forcing. The results of this study generally support the idea of the dependence of the PWS population on the Eastern local population, the importance of spatial complexity and metapopulation structure, and higher survival of recruits from the East and possibly North. The metapopulation theory posed in Chapter 1, with the existence of at least two distinct local populations in PWS (Eastern and Southwestern encompassing the Montague area), is more appropriate for PWS than a single stock theory.

Because of the dependence of PWS total herring recruitment and the level of recruit-per spawner on Eastern herring production, factors affecting the proportion of age-3 recruiting to spawn may determine year-class strength for PWS as a whole. Pacific herring in PWS are considered only partially recruited by age-3 and are not included in age-structured management models until age four (Funk 1995). In this study, differences in patterns of significant variables and functional responses for age-3 versus age-4 models were observed. Age-3 recruitment variables may represent the variation in the proportion maturing to spawn, rather than total abundance of the cohort as in age-4 models. Factors affecting the maturation process may differ slightly from those affecting survival. Eastern age-3 recruitment models were particularly different from the age-4 local recruitment models. Eastern age-3 recruitment had worse fit models than other regions probably because factors directly affecting proportion maturing were not included. Only Eastern age-3 models showed best-fit models with zooplankton and during spring +1 lag, corresponding to the end of the first overwinter period and main zooplankton bloom in PWS. Sexual maturity is size-dependent (Hay and Brett 1988) and

therefore factors affecting growth, such zooplankton production, are important. In addition, the local region producing best fit Eastern age-3 recruitment models was the PWS Entrance, the main transport site for large GOA copepods into the sound (Cooney et al. 2001). The zooplankton variable used in this study came from a single site in southwestern PWS and may therefore poorly represent feeding conditions at eastern nursery sites. Eastern sites may be more heavily dependent on GOA transport for food. In contrast, zooplankton was not a significant variable in Montague age-3 models; oceanographic conditions during the late larval and early juvenile stages produced better model fits. For the Northern regions, the best age-3 models occurred with –1 lag variables corresponding to conditions of the adults prior to cohort. Given the dependence of PWS age-4 recruitment on Eastern age-3, predictions of both local and soundwide recruitment may improve if factors affecting the proportion maturing to spawn, such as eastern zooplankton transport or production and eastern PWS oceanographic measurements, are included.

Critical Life History Periods

Eight key mechanistic, spatially explicit processes were inferred from the identified critical life history periods, geographic differences in response, and best model fit environmental factors. The first process was enhancement of juvenile survival in the spring following the first overwintering period, with an early zooplankton bloom and sustained prey densities effected by wind and a relaxation of downwelling at the entrance to PWS. The second process was negative effects on recruitment from instability of surface waters during late summer resulting in less than optimal feeding

conditions for adults and effects on reproductive success. Third, larval survival improves with maintenance of a mixed layer, some wind mixing, and wind-driven transport to ensure a continued source of nutrients for a healthy bloom and arrival at a nearshore rearing location. Fourth, maintenance of oceanic conditions and tidal mixing (high salinity, low temperatures) in the nearshore refuge zones at the nurseries provide continued prey for juvenile growth and survival. Fifth, increased oceanic mixing and currents interfere with the intersection of age-2 juveniles with adult schools. For the sixth process in the fall prior to the cohort year, increased wind mixing (maintaining oceanic salinity values) and sustained summer SST values, at a time when cold freshwater input is at an annual maximum, enhances adult feeding and condition and thus reproductive success. Seventh, in contrast to fall conditions for the adults, wind mixing in the nearshore nurseries areas has negative consequences for age-0 juvenile survival possibly by reducing nearshore prey resources. The eighth and final process occurs in the fall, after the age-2 juveniles have joined adult schools. As with the adults (fall –1 lag, sixth process), sustained summer SST values may enhance growth, condition and thus survival. However, unlike the adults these immature herring show geographically mixed responses to high salinity and variance in salinity and SST. Because age-2 herring are the smallest individuals in the size-structured adult schools, density-dependent competition or size-dependent mortality may become more important than other periods.

The enhancement of juvenile survival, in the spring following the first overwintering period, with an early zooplankton bloom and sustained prey densities

effected by wind and a relaxation of downwelling at the entrance to PWS, was inferred from the spring +1 lag responses. These responses included the positive correlations to zooplankton (Table 11, Figure 14b), wind variables, the upwelling index, and SST. According to PWS overwintering studies, these juveniles are near the end of their energetic reserves; the timing and magnitude of the zooplankton bloom could be critical for survival (Foy and Paul 1999). High spring SST values may indicate early stratification (Royer 1982) and an early bloom (Cooney et al. 2001). Some wind mixing would result in maintaining nutrients to prolong the bloom (Eslinger et al. 2001) and a relaxation in the downwelling (more positive upwelling index values) at the entrance to PWS aid in retention (Cooney et al. 2001) of the large, nutritionally superior oceanic copepods (Foy and Norcross 1999) within PWS. The wind variables showed worse model fits than the local SST and salinity variables; however, as with the zooplankton variables, this may reflect this distance between the measurement (NGOA) and the effect of forcing in local regions of PWS. Localized wind measurement would probably result in improved model fits with recruitment. Early and sustained availability of high quality prey probably enhances overwinter survival of the juveniles. Eastern recruitment was more highly correlated, with lower AIC values, to increasing spring SST and zooplankton than Northern and Montague. The Eastern area is closer to the entrance to PWS where the large oceanic copepods enter from the GOA (Cooney et al. 2001). In addition, early spring stratification and high SST may occur more frequently in the protected, ice-free fjords and embayments of the East, compared to the Northern and Montague area (see Gay and Vaughan 2001). Therefore, this period may be more critical

to survival of recruits from the East and thus to PWS recruitment as a whole, than for the other two regions.

The negative effects of surface water instability on reproductive success and recruitment, during late summer prior to the cohort year, were inferred from the late summer -1 lag period where recruitment was negatively correlated with increasing variance in SST and salinity but positively correlated to SST. Growth and condition previous to spawning modify reproductive processes indirectly through affects on lipid reserves needed to produce eggs (Tanasichuk and Ware 1987; Hay and Brett 1988; Winters et al. 1993; and Winters and Wheeler 1996) and the temperature exposure history of Pacific herring females affects spawn timing, egg size, and fecundity (Hay 1985; Kay and Kronlund 1987; Ware and Tanasichuk 1989). For PWS herring, prolonged zooplankton blooms in late summer may enhance reproduction by resulting in good adult condition going into the overwinter period prior to spawning (Paul et al. 1996). During late summer, if the upper surface is unstable due to frequent turnover, feeding conditions may be sub optimal and adult condition reduced. Alternately, higher than normal SST in late summer may indicate prolonged stratification and a continued bloom. Because the late summer –1 lag period was a key period for recruitment in PWS, adult condition the fall before spawning and spawn timing are likely important to successful recruitment. The impacts of sub-optimal adult condition or spawn timing are probably observable during the egg and larval stage with reduced survival of one or both (see Chapter 1).

Geographic differences in enhancement of larval survival with maintenance of a healthy bloom, was inferred from the late summer 0 lag and the positive correlations to SST, wind mixing, variance in wind speed, and wind events and negative correlations to increasing salinity (Table 11; Figure 14b). This period corresponds to larval drift through metamorphosis. High temperatures and wind mixing may indicate the continued presence of a mixed layer with an influx of nutrients yet shallow enough to maintain ocean productivity and promote larval feeding and growth (Bakun 1996; Gargett 1997). These proposed processes fit in with the dome-shaped, optimal environmental window theory (Cury and Roy, 1989; Gargett, 1997) where production is optimized at a balance between upwelling and turbulence. Some wind mixing is good for nutrient influx, but too much reduces productivity partially by increasing the mixed layer depth below the euphotic zone. Montague recruitment had best-fit models during this larval drift period and was more highly correlated to the wind variables than the other two regions. The Montague area is more exposed to GOA weather and storms (Neibauer et al. 1994; Gay and Vaughan 2001) and it is possible that stratification and the associated plankton production in herring rearing areas are more wind dependent than in the fjords of the east and north. For the Montague region, there may also be a higher risk of advection of larvae (Chapter 1) that would occur at the 0 lag for variables. For recruits from Montague, the positive correlation to wind variables may correspond with wind-driven transport to favorable nursery locations. The stronger association with wind forcing would reduce the influence of other variables, such as zooplankton on Montague survivors. Localized measurements of wind in the Montague region would probably

improve model fits of local recruitment to wind variables. Processes affecting recruitment success at Montague may be more similar to Bering Sea herring than other local populations in PWS. Bering Sea herring recruitment success is heavily dependent on wind-driven transport during the larval stage (Wespestad 1991).

Maintenance of oceanic conditions and tidal mixing (high salinity, low temperatures) in the nearshore nursery refuge zones, providing continued prey for growth and survival, was inferred from the late summer +1 lag period, the positive correlations with salinity and negative correlations with SST (Table 11). In PWS, juveniles are found tightly schooled and mainly nearshore (< 1 km) in the upper 20 m of the water column (Stokesbury et al. 1999a). This shoreward-shallow water preference is predicted by behavioral energetic models (Crowder and Magnuson 1983; Ware 1985) as juvenile herring precariously balance between feeding and being eaten (Walters and Juanes 1993). During daylight hours, schooling and the nearshore refuge areas become the main predator defense along with increase in size, since predation rates are size-dependent (Werner et al. 1983; Walters and Juanes 1993). Within these refuge zones, high SST increases metabolic activity requiring higher feeding levels (Foy and Paul 1999) and lack of zooplankton can impact growth and thus survival. Large amounts of freshwater input to the nearshore can create a highly stratified wedge-shaped layer with low surface salinity, increased SST from solar heating, and very little mixing with offshore, saline oceanic water (Gay and Vaughan 2001). If high quality (in terms of energetic content, Foy and Norcross 1999) oceanic zooplankton are prevented from mixing into this nearshore area, food may become depleted for the herring residing

there. During this period, high salinity and low SST may indicate increased mixing with oceanic waters causing advection of oceanic zooplankton into the refuge areas, along with lowered metabolic stress for the juveniles. These conditions may enhance growth and survival, producing the positive effects observed on recruitment.

Increased mixing and ocean currents that interfere with the ability of juveniles to find and join with adult schools was inferred from the late summer +2 lag and the negative responses to variation in salinity and SST (Table 11). This process of "joining" and spatial learning, where adults lead new members to the overwintering and spawning areas, is critical for maintenance of a local population (Fernö et al.1998). The strong and negative correlations of recruitment with variance in salinity and SST during this period may indicate unstable surface waters and increased ocean currents that act as a barrier to juveniles leaving nursery areas and joining adult schools. Alternately, these ocean conditions may affect the distribution of adults resulting in an increased distance between juvenile and adult schools and impairing the process of joining.

The enhancement of reproductive success from increased mixing (maintaining oceanic salinity values) and summer SST values sustained into the fall, at a time when cold freshwater input is at an annual maximum, was inferred from the fall –1 lag and positive correlations of recruitment to salinity, SST, wind variables but negative correlations to variance in salinity (Table 11). Freshwater input from ice and snow melt as well as rain is at a maximum during the fall in the Gulf of Alaska (Royer 1982). Storm and wind events keep the surface waters well-mixed resulting in mixing down the cold fresh water (Gay and Vaughan 2001) and mixing up of any remaining planktonic

food sources. The sustained higher summer SST values may keep adult metabolisms and feeding rates up enhancing condition during the fall prior to spawning. This may result in higher reproductive success and increased survival of recruits. If surface waters become less salty and colder earlier in the fall, feeding rates may decrease and affect adult reproductive condition.

In contrast to enhancement of condition for adults, excessive mixing down of surface waters may reduce critical prey resources for age-0 juveniles entering their first overwinter period in the nearshore nursery areas. This idea is similar to the dependence of anchovy larval survival on concentrated food particles and the destructive effects of storm events on that prey field (Lasker 1975, 1978). In PWS, the negative consequence of excessive mixing was inferred from the fall 0 lag model results and the mainly negative correlations to salinity, SST and variance in SST (Table 11). Continued stratification, induced by increased freshwater input during the fall (over other months; Royer 1982; Gay and Vaughan 2001) may help keep any remaining zooplankton, from the late summer bloom, concentrated in the upper surface waters. In addition, cooler temperatures may help keep metabolic needs low at a time when food resources are dwindling. Higher SST could induce stress and starvation. Although most local recruitment variables were negatively correlated to salinity, SST and variance in SST, the spatial differences in response may represent diversity in local conditions among nursery areas. Growth rates (Stokesbury et al. 1999b) and condition (Paul and Paul 1999) are highly variable among nursery sites in PWS. A successful year class may

therefore depend on maintenance of fall stratification and lower SST in a majority of nursery bays.

Competition and access to food in size-structured schools may affect age-2, immature and adult herring differently. Enhanced age-2 survival during the fall with sustained summer SST values was inferred from the positive correlations to SST during the fall +2 lag period (Table 11). However, negative effects on survival from competition with adults were inferred, over the same period, from the assumption of overlapping distribution with adult schools and the variable response to salinity and variance in salinity and SST. By fall, the age-2 recruits have joined adult schools (Stokesbury et al. 1999a) and probably experience similar physical conditions and prey fields. As with the adults (fall –1 lag, sixth period), sustained summer SST keep metabolism and feeding rates high enhancing growth, condition and thus survival. However, unlike the adults these immature herring show geographically mixed responses to high salinity and variance in salinity and SST. Because age-2 herring are the smallest individuals in the adult schools, size-structuring predicted by behavioral bioenergetic models (Werner and Hall 1977; Hughes and Grand 2000) probably restricts movement to deeper areas of the water column with prey that are occupied by larger individuals. This results in density-dependent competition and size-dependent mortality that becomes a more deterministic process for survival during times of low versus high prey density. By fall, prey fields have been mixed deeper (Cooney et al. 2001) and the size-structuring may be a disadvantage for the relatively small age-2 herring.

It is clear that multiple critical periods, each with varying key processes, must be bridged for young herring to join and ultimately spawn with existing adult schools. Recruitment models for PWS recruitment or recruit-per-spawner production must include variables from more than one period to retain predictive power. Geographic differences in recruitment response to key periods and processes reflect the spatial complexity and the need for collection of local meteorological and oceanographic information in order to maintain the explanatory power of those models. The results presented here have identified key times and places for collection of data to parameterize models. This is the first step if management or monitoring is to include ecosystem-based population monitoring of Pacific herring.

Applicability of Study

The two types of environmental models, parametric linear and non-parametric gams, developed in this study are immediately applicable for two types of uses. First, linear models could be easily and immediately adopted and used for single-species herring management by fisheries managers. The linear models do not require sophisticated statistical programs and input variables are relatively simple and inexpensive to measure (i.e. local SST and salinity). The linear models would be employed to predict PWS recruitment as a whole and linked to age-structured-analysis (asa) models, currently used to forecast harvestable surplus (Funk 1995). The abundance of age-3 and –4 herring is not predicted by the asa forecast model and the addition of recruitment prediction could greatly improve the asa's utility and accuracy. A more accurate forecast would assist the fishing industry in predicting fishery staging needs

and cost. Specifically for PWS, using the best model fit values shown in Table 10 for PWS total age-3 and –4 and recruit-per-spawner age-3 and –4, the only environmental data need is a time series of SST and salinity values for the upper 20 m for Northeastern (NE) and Southeastern (SE) PWS (see Figure 4) from July through November. Ideally, weekly SST and salinity would be collected from 10 or more stations in each local region within PWS. From this information, an annual mean and variance is estimated for each local region for each of the two periods, late summer (July-August) and fall (September-November). Each mean is subtracted from the long-term mean (20 yrs plus) for each period to provide a normalized value. Then the series are entered into the following equation using least squares fitting:

$$\ln(R) = a + \sum_{j=0}^{p} B_j E_j + \varepsilon \quad \text{or} \quad \ln(R/S) = a + \sum_{j=0}^{p} B_j E_j + \varepsilon \text{ (modified from Eqs. 1 and 2)}$$

The following is a list of variables (from Table 10) representing E_j for each of the 4 PWS recruitment indices and cohort year x to be predicted:

1) PWS total age-3 recruitment: E_1 = NE late summer variance in salinity year $x-1$, E_2 = NE late summer variance in SST year $x-1$, E_3 = NE late summer SST during year x, and E_4 = NE fall variance in salinity year $x-1$

2) PWS recruit-per-spawner age-3: E_1 = NE late summer variance in salinity year $x-1$, E_2 = NE late summer variance in SST year $x-1$, E_3 = NE late summer SST during year $x+1$, E_4 = NE fall variance in salinity year $x-1$, and E_5 = NE fall salinity in year x

3) PWS total age-4 recruitment: E_1 = NE late summer SST year $x-1$ and E_2 = SE late summer salinity in year $x+1$

4) PWS recruit-per-spawner age-4: E_1 = SE late summer salinity year $x+1$, E_2 = NE fall salinity in year x, E_3 = NE fall salinity in year $x+2$

For other regions in the North Pacific, specific recruitment relations should be estimated from local oceanographic or other variables known to be important for the local population of interest.

Secondly, spatially-explicit gams could be used to parameterize ecosystem-based models. The need for ecosystem-based models is increasing and output from non-parametric spatially-explicit gams are useful in defining the functional responses needed for model parameterization and in pinpointing the key times and places for environmental measurements. The shift in fisheries and marine resource management from single-species to ecosystem approaches will likely require the inclusion of key forage species such as herring, cost-effective tools, a better understanding of long-term environmental effects, and an increasing reliance on models (Beamish and Mahnken 1999). Resource managers are often faced with declining budgets while at the same time experiencing an increased demand for more ecologically based information. The complex array of issues requiring ecosystem-based information include multi-species interactions, by-catch issues, implementation of marine protected areas, and endangered species protection, especially those feeding on key forage fish species such as herring (Link 2002). Often, the need for information is a matter of avoiding the courtroom rather than a choice. Predictive environmental models of herring recruitment would be useful because they include life stages important for ecosystem processes (e.g. larvae and juveniles) not normally addressed in herring management models (Williams and Quinn

1997). An ecosystem-based conceptual model for herring year-class formation was formulated in Chapter 1. By focusing on parameterization of portions of the conceptual model matching the critical periods identified in and the results from this study, an ecosystem model for the PWS herring population could be realized with a small amount of effort. According to this study, the key to producing an ecosystem-based model with a high degree of explanatory power is monitoring local conditions in the times and places identified (Figure 19). In PWS, and other locations in the Northeast Pacific, the key processes probably occur in spring, late summer, and early fall. The data needed for each critical period varies and the best fits occur with the local hydrographic information. However, localizing data collections of zooplankton, especially during the spring bloom, and wind measurements, a relatively inexpensive data source, may result in improving the overall explanatory power of these ecosystem-based recruitment models. By restricting data collections to localized times and places and given that many of the variables are inexpensive to collect, ecosystem-based modeling and monitoring of Pacific herring should be affordable to any management program in existence.

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Table 3.1. Sources of data used in the analysis of environmental effects on herring recruitment in Prince William Sound, Alaska categorized by variable type and region of applied forcing. All variables were tested as –1, 0, +1 and +2 yr lags to the cohort year. The total number of variables created in each category is given.

Data Type	Period	Sources and Total No. Variables
Herring Variables		
Spawn Index, PWS Regional & Sound-wide		
Total Annual PWS herring spawn in mile-day; reported in five regions (Figure 1: SE, NE, NS, NI, MT) Reduced to 3 regions during data exploration to: Eastern Spawn (**ESPN**) Northern Spawn (**NSPN**) Montague Spawn (**MTSPN**) and one composite variable: PWS Total Spawn (**TOTSPN**)	1973-1999	**Total Spawn Variables = 4** Biggs et al. 1992; Brady *et al.* 1987 Steve Moffit and John. Wilcock, personal communications, ADFG, Cordova; Fritz Funk, ADF&G Juneau, personal communication
Recruitment, PWS Regional & Sound-wide		
Age 3 and 4 region-specific peak biomass from aerial surveys (reported in same regions as spawn) multiplied by region-specific proportion-weight by age (age composition) to allocated biomass to cohorts (age 3 and 4); 5 regions reduced to 3 during data exploration to: 1.Eastern area recruitment (**E3** and **4**) 2. Northern area recruitment (**N3** and **4**) 3. Montague area recruitment (**MT3** and **4**) and two composites: 4. PWS total recruitment (**TOT3** and **4**) 5. Recruit per Spawner (**R/S 3** and **4**)	1973-1999	**Total Recruitment Variables = 10**
Sound-wide Environmental Variables		
1) *Climate, North Pacific*		**Total # Variables 72**
Seasonal Pacific Decadal Oscillation (PDO)	1900-1999	Mantua et al. 1997 Total PDO Variables = 4 X 4 lags = 16
Seasonal El Niño-Southern Oscillation (ENSO)	1870-1998	Enfield and Mestas-Nuñez, 1999
Seasonal Pacific Inter-Decadal Oscillation (PIDO)	1856-1998	Total ENSO, PIDO, PMDO = 4 X 4
Seasonal Pacific Multi-Decadal Oscillation (PMDO)	1856-1998	lags X 3 types = 48
Annual Aleutian Low Pressure Index (ALPI)	1901-1998	Beamish and Bouillon, 1993 Total ALPI = 1 X 4 lags = 4
Annual Atmospheric Forcing Index (AFI)	1900-1999	MacFarlane et al. 2000 Total AFI Variables = 1 X 4 lags = 4
2) *Fresh Water Discharge, North Gulf of Alaska (N GOA)*		**Total # Variables 48**
Monthly Fresh water discharge (FWD)	1931-1999	Royer 1982; University of Alaska (UAF), Institute of Marine Science (IMS) database;Total FWD Variables = 12 X 4 lags = 48

Table 3.1 Continued.

Sound-wide Environmental Variables Continued		
3) *Upwelling, N GOA*		**Total # Variable 48**
Monthly Bakun Upwelling (**UW**) Index	1946-1999	Bakun 1973, 1975; Total UW Variables = 12 X 4 lags = 48
4) *Wind, N GOA*		**Total # Variables 120**
Monthly Middleton Island meteorological data; Combined in following periods: Jan.-Feb., Mar.-Apr., May-June. July excluded, Aug. by itself, Sept.-Nov. combined, Dec. by itself. Wind Variables over Those Periods: 1. Mean Wind speed (**MW**) 2. Mean Wind cubed ($\mathbf{MW^3}$) representing wind mixing 3. Variance of Mean Wind speed (**VW**) 4. Mean # High Speed Wind Events (**HS WE**) between 25-35 knots 5. Mean # Gale Force Wind Events (**GF WE**) over 35 knots	1972-1999	Total Wind Variables = 6 periods X 5 types X 4 lags = 120 National Climate Data Center, North Carolina **Total # Variables 96** Total Pr. and A. Variables = 12 periods X 2 types X 4 lags = 96
5) and 6) *Precipitation and Air Temperatures, PWS*		
Monthly Precipitation and air temp. PWS sites (Pr & A)	1972-1999	
7) *Zooplankton, PWS*		**Total # Variables 8**
Annual zooplankton settled volumes from SW PWS; zoop. variables included were: 1. Average Zoop. Density over 6 wk period (**AVEZOOP**) 2. Peak Zoop. Density over 6 wk period (**PKZOOP**)	1980-1999	Prince William Sound Aquaculture Corporation (Cordova, Alaska) plankton watch program Total Zooplankton Variables = 2 types X 4 lags = 8
Local and Sound-wide Variables		
8) *PWS Hydrography, PWS oceanographic localities and PWS composite*		**Total # Variables 640**
PWS hydrographic data queried for 7 regions (Figure 4: **SE, NE, NS, CS, MS, SW, ENT**) plus **PWS** composite; Calculated over 5 bi-monthly periods: Jan.-Feb. (**JF**), Mar-Apr. (**MA**), May-Jun. (**MJ**), Jul.-Aug. (**JA**), and Sept.-Oct. (**SO**). For four variables calculated for the upper 20 m: 1.Mean Temp.C (**T**) 2. Mean Salinity (**S**) 3. Variance in Temp. (**VT**) 4. Variance in Salinity (**VS**)	1973-1999	UAF IMS database Total PWS Hydrographic Variables = 7 regions X 5 time periods X 4 types X 4 lags = 640 ; 560 regional 80 PWS sound-wide
9) Fishing Mortality – All PWS Districts Combined (ADFG unpublished data)		**1**
Total Sound-wide Variables		**392 (Type 1-7) + 81 (Type 8-9) = 473**
Total PWS Local Variables		**(all Type 8) 560**
Total Environmental Variables		**1,033**
Grand Total		**1,047**

Table 3.2. Summary statistics for variables significantly correlated to combined and individual recruitment variables categorized by 1) season, 2) region for applied forcing (Soundwide = S, Local within PWS = L), 3) lag in years from hatch (cohort year), and 4) type of parameter. Statistics shown include 1) total possible variables included in models (Total V) 2) number of unique variables (Unique V), 3) number of significant variables (V) in the models, 4) percentage of significant variables of those possible (V/Total V), 5) redundancy rate (= #V/# Unique V) representing variables significant to more than one recruitment variable with notably higher values bolded, 6) average p-values of the correlations, 7) average absolute values of the correlation coefficients (r), and 8) average model Akaike Information Criteria (AIC) values from the single parameter general additive model runs with low values representing better model fits.

	All Recruitment Variables Combined							
Season	**Total V Possible X 10 Recruitment Variables**	**# Unique V**	**V**	**%V of Total V**	**Redun. Rate**	**avg. p-value**	**avg. |r|**	**avg. AIC**
Annual	200	1	1	0.5%	1.00	0.050	0.404	146.12
Spring[1]	1920	80	182	9.5%	2.28	0.040	0.665	33.80
Early Summer	1800	63	135	7.5%	2.14	0.048	0.666	39.91
Late Summer	1840	70	169	9.2%	2.41	0.037	0.783	19.14
Fall	2000	82	170	8.5%	2.07	0.043	0.705	31.49
Winter	*2200*	*20*	*48*	*2.2%*	*2.40*	*0.020*	*0.512*	*82.61*
Region								
N Pacific (S)	2160	8	11	0.5%	1.38	0.035	0.447	106.31
North GOA (S)	800	42	99	12.4%	2.36	0.019	0.519	72.86
PWS (S)	800	38	107	13.4%	**2.82**	0.042	0.593	42.75
PWS Entrance (L)	1840	33	57	3.1%	1.73	0.048	0.780	13.42
Central PWS (L)	800	31	68	8.5%	2.19	0.041	0.667	30.42
Montague Strait (L)	800	34	79	9.9%	2.32	0.038	0.706	29.72
Northeast PWS (L)	800	32	61	7.6%	1.91	0.049	0.918	18.78
North Shore (L)	800	32	79	9.9%	2.47	0.044	0.765	24.56
Southeast PWS (L)	800	32	78	9.8%	2.44	0.048	0.818	13.51
Southwest PWS (L)	800	33	66	8.3%	2.00	0.044	0.646	29.71
Lag								
-1	2490	88	204	8.2%	2.32	0.044	0.726	35.89
0	2490	80	175	7.0%	2.19	0.036	0.685	32.49
1	2490	77	203	8.2%	**2.64**	0.038	0.695	27.80
2	2490	70	123	4.9%	1.76	0.044	0.644	45.44
Type								
Herring								
Age3 Herring - L & S[2]	25	5	11	44.0%	2.20	0.001	0.652	51.97
Spawn Magnitude - L & S	40	1	3	7.5%	3.00	0.083	0.315	64.97
Environmental								
Fishing Mortality - S	10	0	0	0.0%	-	-	-	-
Climate - S	360	8	11	3.1%	1.38	0.021	0.519	107.25
Precip. and Air Temp. - Sound-wide	960	0	0	0.0%	-	-	-	-
Fresh Water - S	480	4	6	1.3%	1.50	0.016	0.501	98.40
Upwelling - S	480	10	29	6.0%	**2.90**	0.025	0.481	116.84
Mean Wind - S	240	10	23	9.6%	2.30	0.014	0.557	42.25
Wind Mixing - S	240	5	10	4.2%	2.00	0.017	0.520	54.09
Var. Wind - S	240	6	14	5.8%	2.33	0.018	0.526	42.20
Gale Force Wind Events - S	240	3	5	2.1%	1.67	0.021	0.524	39.93
High Speed Wind Events - S	240	4	12	5.0%	**3.00**	0.014	0.545	55.18
Zooplankton - Soundwide	80	4	17	**21.3%**	**4.25**	0.017	0.621	50.68
Salinity - S	200	7	17	8.5%	2.43	0.041	0.610	34.33
Temperature - S	200	10	24	12.0%	2.40	0.041	0.599	33.50
Var. Salinity - S	200	7	19	9.5%	**2.71**	0.053	0.590	54.66
Var. Temp. - S	200	10	30	15.0%	**3.00**	0.050	0.566	42.88
Total Sound-wide (S)	4415	88	217	4.9%	2.47	0.031	0.554	58.10
Salinity - L	1400	56	115	8.2%	2.05	0.044	0.735	19.48
Temperature - L	1400	60	133	9.5%	2.22	0.046	0.746	19.55
Var. Salinity - L	1400	44	99	7.1%	2.25	0.044	0.773	38.81
Var. Temp. - L	1400	68	141	10.1%	2.07	0.044	0.768	18.43
Total PWS Regional (L)	5620	228	488	8.7%	2.14	0.044	0.747	25.03
Total Environmental (L+S)	9970	316	705	7.1%	2.28	0.040	0.692	34.38
Total Herring	65	6	14	21.5%	2.33	0.040	0.692	34.38
Grand Total (L + S + Herring)	**10035**	**322**	**719**	**7.2%**	**2.23**	**0.039**	**0.709**	**13.91**

1. Zooplankton categorized in Spring, but spans spring to early summer
2. Age-3 Variables (5) times 5 Age-4 models

Table 3.2. Continued. Characterization of environmental predictor variables significantly correlated to the Eastern area age-3 and -4 recruitment with the best fitting variables (lowest AIC) in each category bolded.

	Eastern Area Age 3 Recruits						Eastern Area Age 4 Recruits					
Season	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC
Annual	20	0	0.0%	-	-	-	20	0	0.0%	-	-	-
Spring	192	26	13.5%	0.031	0.666	**73.80**	192	15	7.8%	0.038	0.640	20.32
Early Summer	180	19	10.6%	0.056	0.688	113.37	180	18	10.0%	0.037	0.639	24.83
Late Summer	184	11	6.0%	0.039	0.714	103.23	184	12	6.5%	0.046	0.824	**6.82**
Fall	200	18	9.0%	0.039	0.651	116.69	200	16	8.0%	0.049	0.676	15.60
Winter	220	7	3.2%	0.007	0.563	192.49	220	10	4.5%	0.021	0.526	38.26
Region												
N Pacific	216	1	0.5%	0.016	0.526	101.19	216	0	0.0%	-	-	-
North GOA	80	21	26.3%	0.015	0.535	131.19	80	23	28.8%	0.019	0.531	37.02
PWS	80	10	12.5%	0.040	0.600	76.84	80	9	11.3%	0.064	0.533	26.16
PWS Entrance	184	3	1.6%	0.017	0.865	**19.52**	184	2	1.1%	0.066	0.701	10.31
Central PWS	80	8	10.0%	0.049	0.646	113.54	80	4	5.0%	0.045	0.675	16.46
Montague Strait	80	8	10.0%	0.044	0.701	107.15	80	8	10.0%	0.044	0.706	12.34
Northeast PWS	80	10	12.5%	0.058	0.881	97.41	80	6	7.5%	0.052	0.801	**7.27**
North Shore	80	7	8.8%	0.058	0.700	143.91	80	7	8.8%	0.037	0.816	**7.38**
Southeast PWS	80	9	11.3%	0.043	0.714	95.75	80	9	11.3%	0.045	0.873	**4.29**
Southwest PWS	80	4	5.0%	0.038	0.659	91.02	80	3	3.8%	0.045	0.643	19.95
Lag												
-1	249	24	9.6%	0.052	0.704	124.72	249	17	6.8%	0.041	0.741	**11.65**
0	249	17	6.8%	0.038	0.697	81.20	249	16	6.4%	0.040	0.649	22.94
1	249	18	7.2%	0.022	0.673	**73.91**	249	20	8.0%	0.044	0.718	15.37
2	249	14	5.6%	0.048	0.613	158.44	249	10	4.0%	0.038	0.549	29.52
Type												
Age3 - Local and Soundwide	-	-	-	-	-	-	5	2	40.0%	0.001	0.670	31.13
Spawn - Local and Soundwide	4	1	25.0%	0.117	0.329	98.85	4	1	25.0%	0.077	0.224	53.69
Fishing Mortality - Soundwide	1	0	0.0%				1		0.0%			
Climate - Soundwide	36	1	2.8%	0.016	0.526	101.19	36	0	0.0%	-	-	-
Precip. and Air Temp. - Soundwide	96	0	0.0%				96		0.0%			
Fresh Water - Soundwide	48	1	2.1%	0.035	0.432	385.41	48	0	0.0%	-	-	-
Upwelling - Soundwide	48	6	12.5%	0.014	0.507	349.86	48	5	10.4%	0.024	0.482	43.21
Mean Wind - Soundwide	24	13	54.2%	0.015	0.548	**42.63**	24	10	41.7%	0.013	0.566	34.39
Wind Mixing - Soundwide	24	0	0.0%	-	-	-	24	0	0.0%	-	-	-
Var. Wind - Soundwide	24	1	4.2%	0.011	0.528	**50.45**	24	3	12.5%	0.012	0.558	35.23
Wind Events - Soundwide	24	1	4.2%	0.002	0.627	59.08	24	5	20.8%	0.030	0.494	37.17
Zooplankton - Soundwide	8	2	25.0%	0.007	0.636	**30.65**	8	2	25.0%	0.024	0.618	19.89
Salinity - Local and Soundwide	160	15	9.4%	0.039	0.780	72.84	160	9	5.6%	0.058	0.708	**10.30**
Temperature - Local and Soundwide	160	16	10.0%	0.052	0.702	51.60	160	15	9.4%	0.051	0.721	**14.11**
Var. Salinity - Local and Soundwide	160	15	9.4%	0.061	0.665	185.64	160	5	3.1%	0.054	0.798	**10.99**
Var. Temp. - Local and Soundwide	160	10	6.3%	0.035	0.743	64.25	160	17	10.6%	0.044	0.732	**12.66**
Grand Total	**977**	**73**	**7.5%**	**0.041**	**0.677**	**108.52**	**982**	**63**	**6.4%**	**0.041**	**0.680**	**18.54**

Table 3.2. Continued. Characterization of environmental predictor variables significantly correlated to the Northern area age-3 and -4 recruitment with the best fitting variables (lowest AIC) in each category bolded.

	Northern Area Age 3 Recruits						Northern Area Age 4 Recruits					
Season	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC
Annual	20	1	5.0%	0.050	0.404	146.12	20	0	0.0%	-	-	-
Spring	192	16	8.3%	0.043	0.622	61.85	192	19	9.9%	0.043	0.638	70.48
Early Summer	180	18	10.0%	0.055	0.595	57.87	180	17	9.4%	0.043	0.651	48.07
Late Summer	184	14	7.6%	0.033	0.837	**26.44**	184	19	10.3%	0.034	0.799	**38.37**
Fall	200	11	5.5%	0.045	0.660	52.00	200	14	7.0%	0.050	0.679	52.50
Winter	220	10	4.5%	0.021	0.512	124.21	220	11	5.0%	0.021	0.507	135.44
Region												
N Pacific	216	9	4.2%	0.014	0.528	123.83	216	13	6.0%	0.013	0.557	126.11
North GOA	80	8	10.0%	0.026	0.497	124.48	80	7	8.8%	0.026	0.482	140.07
PWS	80	15	18.8%	0.053	0.522	78.30	80	12	15.0%	0.035	0.598	78.05
PWS Entrance	184	3	1.6%	0.083	0.720	21.09	184	6	3.3%	0.056	0.772	21.99
Central PWS	80	2	2.5%	0.043	0.648	44.57	80	4	5.0%	0.030	0.699	44.99
Montague Strait	80	8	10.0%	0.034	0.719	36.30	80	12	15.0%	0.050	0.694	46.12
Northeast PWS	80	6	7.5%	0.044	0.920	**3.46**	80	2	2.5%	0.060	0.928	**8.30**
North Shore	80	6	7.5%	0.045	0.741	27.45	80	9	11.3%	0.050	0.762	23.29
Southeast PWS	80	9	11.3%	0.041	0.796	24.95	80	8	10.0%	0.062	0.790	20.07
Southwest PWS	80	4	5.0%	0.066	0.572	55.97	80	7	8.8%	0.034	0.695	43.03
Lag												
-1	249	17	6.8%	0.046	0.742	**44.75**	249	26	10.4%	0.045	0.667	71.66
0	249	13	5.2%	0.045	0.696	46.85	249	17	6.8%	0.038	0.702	**45.72**
1	249	11	4.4%	0.057	0.569	58.34	249	14	5.6%	0.037	0.726	50.82
2	249	18	7.2%	0.043	0.629	58.58	249	14	5.6%	0.053	0.611	50.39
Type												
Age3 - Local and Soundwide	-	-	-	-	-	-	5	2	40.0%	0.002	0.495	129.42
Spawn - Local and Soundwide	4	0	0.0%	-	-	-	4	0	0.0%	-	-	-
Fishing Mortality - Soundwide	1	0	0.0%	-	-	-	1	0	0.0%	-	-	-
Climate - Soundwide	36	9	25.0%	0.014	0.528	123.83	36	13	36.1%	0.013	0.557	126.11
Precip. and Air Temp. - Soundwide	96	0	0.0%	-	-	-	96	0	0.0%	-	-	-
Fresh Water - Soundwide	48	1	2.1%	0.028	0.457	131.96	48	0	0.0%	-	-	-
Upwelling - Soundwide	48	6	12.5%	0.028	0.489	131.87	48	5	10.4%	0.029	0.459	145.78
Mean Wind - Soundwide	24	2	8.3%	0.013	0.551	100.00	24	1	4.2%	0.006	0.594	115.02
Wind Mixing - Soundwide	24	0	0.0%	-	-	-	24	0	0.0%	-	-	-
Var. Wind - Soundwide	24	0	0.0%	-	-	-	24	0	0.0%	-	-	-
Wind Events - Soundwide	24	0	0.0%	-	-	-	24	1	4.2%	0.031	0.482	136.57
Zooplankton - Soundwide	8	4	50.0%	0.044	0.528	93.33	8	3	37.5%	0.004	0.690	84.41
Salinity - Local and Soundwide	160	10	6.3%	0.059	0.659	41.69	160	9	5.6%	0.060	0.679	41.48
Temperature - Local and Soundwide	160	8	5.0%	0.040	0.767	**26.79**	160	20	12.5%	0.044	0.699	42.72
Var. Salinity - Local and Soundwide	160	7	4.4%	0.056	0.738	**26.85**	160	10	6.3%	0.062	0.763	**25.53**
Var. Temp. - Local and Soundwide	160	23	14.4%	0.047	0.692	40.49	160	18	11.3%	0.040	0.725	41.88
Grand Total	**977**	**59**	**6.0%**	**0.047**	**0.665**	**51.97**	**982**	**71**	**7.2%**	**0.044**	**0.676**	**57.14**

Table 3.2. Continued. Characterization of environmental predictor variables significantly correlated to the Montague area age-3 and -4 recruitment with the best fitting variables (lowest AIC) in each category bolded.

	Montague Area Age 3 Recruits						Montague Area Age 4 Recruits					
Season	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC
Annual	20	0	0.0%	-	-	-	20	0	0.0%	-	-	-
Spring	192	24	12.5%	0.044	0.679	29.14	192	20	10.4%	0.042	0.696	20.62
Early Summer	180	12	6.7%	0.055	0.711	26.15	180	15	8.3%	0.049	0.673	22.49
Late Summer	184	26	14.1%	0.032	0.763	**19.63**	184	16	8.7%	0.032	0.761	**18.32**
Fall	200	28	14.0%	0.039	0.711	28.41	200	19	9.5%	0.040	0.754	21.70
Winter	220	1	0.5%	0.022	0.497	68.93	220	3	1.4%	0.020	0.506	78.19
Region												
N Pacific	216	0	0.0%	-	-	-	216	0	0.0%	-	-	-
North GOA	80	10	12.5%	0.015	0.512	72.00	80	8	10.0%	0.014	0.558	67.01
PWS	80	11	13.8%	0.050	0.614	34.34	80	8	10.0%	0.028	0.669	32.81
PWS Entrance	184	12	6.5%	0.056	0.757	19.48	184	9	4.9%	0.035	0.786	13.24
Central PWS	80	10	12.5%	0.023	0.702	21.91	80	10	12.5%	0.042	0.667	21.43
Montague Strait	80	8	10.0%	0.028	0.716	24.67	80	8	10.0%	0.050	0.723	11.43
Northeast PWS	80	10	12.5%	0.055	0.907	**4.78**	80	5	6.3%	0.056	0.906	**4.77**
North Shore	80	10	12.5%	0.042	0.765	14.08	80	6	7.5%	0.041	0.763	17.33
Southeast PWS	80	11	13.8%	0.047	0.829	**8.26**	80	8	10.0%	0.044	0.810	**8.94**
Southwest PWS	80	9	11.3%	0.041	0.615	40.06	80	11	13.8%	0.050	0.647	24.25
Lag												
-1	249	25	10.0%	0.040	0.762	21.02	249	15	6.0%	0.049	0.727	**12.73**
0	249	16	6.4%	0.045	0.642	36.10	249	24	9.6%	0.034	0.722	28.13
1	249	32	12.9%	0.036	0.727	27.98	249	21	8.4%	0.040	0.697	24.52
2	249	17	6.8%	0.046	0.706	**18.39**	249	13	5.2%	0.038	0.704	23.75
Type												
Age3 - Local and Soundwide	-	-	-	-	-	-	5	2	40.0%	0.001	0.646	66.22
Spawn - Local and Soundwide	4	0	0.0%	-	-	-	4	0	0.0%	-	-	-
Fishing Mortality - Soundwide	1	0	0.0%	-	-	-	1	0	0.0%	-	-	-
Climate - Soundwide	36	0	0.0%	-	-	-	36	1	2.8%	0.002	0.609	71.80
Precip. and Air Temp. - Soundwide	96		0.0%	-	-	-	96		0.0%	-	-	-
Fresh Water - Soundwide	48	3	6.3%	0.009	0.529	73.10	48	1	2.1%	0.006	0.580	50.43
Upwelling - Soundwide	48	0	0.0%	-	-	-	48	0	0.0%	-	-	-
Mean Wind - Soundwide	24	1	4.2%	0.016	0.506	68.79	24	2	8.3%	0.028	0.497	81.30
Wind Mixing - Soundwide	24	1	4.2%	0.021	0.489	74.53	24	20	83.3%	0.039	0.719	16.91
Var. Wind - Soundwide	24	2	8.3%	0.020	0.492	75.51	24	1	4.2%	0.001	0.649	43.99
Wind Events - Soundwide	24	3	12.5%	0.016	0.517	68.79	24	2	8.3%	0.007	0.597	57.45
Zooplankton - Soundwide	8	0	0.0%	-	-	-	8	0	0.0%	-	-	-
Salinity - Local and Soundwide	160	25	15.6%	0.037	0.745	20.13	160	18	11.3%	0.041	0.737	20.85
Temperature - Local and Soundwide	160	16	10.0%	0.047	0.745	**19.47**	160	1	0.6%	0.037	0.436	92.33
Var. Salinity - Local and Soundwide	160	20	12.5%	0.049	0.722	22.77	160	8	5.0%	0.045	0.698	22.75
Var. Temp. - Local and Soundwide	160	20	12.5%	0.043	0.749	**19.89**	160	19	11.9%	0.047	0.755	**13.58**
Grand Total	**977**	**90**	**9.2%**	**0.041**	**0.718**	**25.68**	**982**	**73**	**7.4%**	**0.040**	**0.713**	**23.15**

Table 3.2. Continued. Characterization of environmental predictor variables significantly correlated to the PWS total area age-3 and -4 recruitment with the best fitting variables (lowest AIC) in each category bolded.

	PWS Age 3 Recruits						PWS Age 4 Recruits					
Season	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC
Annual	20	0	0.0%	0.000	0.644	26.98	20	0	0.0%	-	-	-
Spring	192	23	12.0%	0.027	0.689	15.83	192	15	7.8%	0.052	0.628	12.85
Early Summer	180	16	8.9%	0.041	0.625	22.45	180	14	7.8%	0.041	0.699	**10.50**
Late Summer	184	25	13.6%	0.034	0.784	**9.43**	184	18	9.8%	0.044	0.745	**10.09**
Fall	200	22	11.0%	0.036	0.703	16.72	200	10	5.0%	0.034	0.715	13.42
Winter	220	1	0.5%	0.061	0.388	51.78	220	6	2.7%	0.020	0.509	32.14
Region												
N Pacific	216	1	0.5%	0.109	0.336	54.10	216	1	0.5%	0.042	0.426	36.17
North GOA	80	10	12.5%	0.019	0.520	43.38	80	10	12.5%	0.019	0.517	31.67
PWS	80	14	17.5%	0.027	0.636	20.71	80	9	11.3%	0.038	0.608	17.68
PWS Entrance	184	7	3.8%	0.038	0.814	**6.23**	184	3	1.6%	0.062	0.704	**5.59**
Central PWS	80	9	11.3%	0.045	0.656	12.72	80	7	8.8%	0.044	0.682	11.24
Montague Strait	80	9	11.3%	0.024	0.697	11.81	80	6	7.5%	0.023	0.694	8.25
Northeast PWS	80	7	8.8%	0.044	0.950	**1.95**	80	4	5.0%	0.037	0.977	**0.66**
North Shore	80	12	15.0%	0.043	0.756	9.40	80	8	10.0%	0.056	0.749	**5.25**
Southeast PWS	80	8	10.0%	0.031	0.838	**5.57**	80	8	10.0%	0.050	0.797	8.61
Southwest PWS	80	10	12.5%	0.037	0.659	16.56	80	7	8.8%	0.058	0.634	11.14
Lag												
-1	249	34	13.7%	0.032	0.751	**11.41**	249	17	6.8%	0.048	0.716	**6.92**
0	249	16	6.4%	0.033	0.740	14.27	249	22	8.8%	0.033	0.637	19.41
1	249	20	8.0%	0.031	0.703	15.06	249	20	8.0%	0.046	0.705	11.45
2	249	11	4.4%	0.053	0.629	17.39	249	4	1.6%	0.035	0.638	18.67
Type												
Age3 - Local and Soundwide	-	0	-	-	-	-	5	2	40.0%	0.000	0.704	22.27
Spawn - Local and Soundwide	4	0	0.0%	-	-	-	4	0	0.0%	-	-	-
Fishing Mortality - Soundwide	1		0.0%				1		0.0%			
Climate - Soundwide	36	1	2.8%	0.109	0.336	54.10	36	1	2.8%	0.042	0.426	36.17
Precip. and Air Temp. - Soundwide	96		0.0%				96		0.0%			
Fresh Water - Soundwide	48	2	4.2%	0.026	0.454	48.40	48	2	4.2%	0.006	0.595	27.70
Upwelling - Soundwide	48	1	2.1%	0.061	0.388	51.78	48	3	6.3%	0.025	0.483	33.73
Mean Wind - Soundwide	24	3	12.5%	0.011	0.552	41.15	24	1	4.2%	0.028	0.479	33.40
Wind Mixing - Soundwide	24	0	0.0%	-	-	-	24	0	0.0%	-	-	-
Var. Wind - Soundwide	24	2	8.3%	0.011	0.549	41.72	24	2	8.3%	0.026	0.485	33.10
Wind Events - Soundwide	24	2	8.3%	0.010	0.577	39.15	24	3	12.5%	0.020	0.508	32.06
Zooplankton - Soundwide	8	2	25.0%	0.006	0.644	26.98	8	1	12.5%	0.007	0.645	19.86
Salinity - Local and Soundwide	160	21	13.1%	0.036	0.713	12.59	160	9	5.6%	0.040	0.696	**9.32**
Temperature - Local and Soundwide	160	17	10.6%	0.041	0.722	10.50	160	15	9.4%	0.042	0.756	**8.89**
Var. Salinity - Local and Soundwide	160	19	11.9%	0.022	0.793	**9.79**	160	9	5.6%	0.046	0.723	**6.15**
Var. Temp. - Local and Soundwide	160	17	10.6%	0.048	0.716	12.24	160	17	10.6%	0.055	0.708	**9.85**
Grand Total	**977**	**81**	**8.3%**	**0.035**	**0.079**	**13.69**	**982**	**63**	**6.4%**	**0.041**	**0.680**	**13.47**

Table 3.2. Continued. Characterization of environmental predictor variables significantly correlated to log-transformed PWS total recruit-per-spawner (R/S) ratios for area age-3 and -4 recruitment with the best fitting variables (lowest AIC) in each category bolded.

	PWS Log R/S Age 3 Recruits						PWS Log R/S Age 4 Recruits					
Season	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC	Total V Possible	V	%V of Total V	ave. p-value	ave. |r|	ave. AIC
Annual	20	0	0.0%	-	-	-	20	0	0.0%	-	-	-
Spring	192	19	9.9%	0.032	0.668	19.12	192	15	7.8%	0.041	0.638	16.63
Early Summer	180	10	5.6%	0.031	0.611	23.32	180	10	5.6%	0.034	0.635	19.40
Late Summer	184	22	12.0%	0.040	0.792	**6.61**	184	12	6.5%	0.039	0.703	**13.87**
Fall	200	29	14.5%	0.043	0.669	16.64	200	16	8.0%	0.044	0.694	**14.97**
Winter	220	3	1.4%	0.014	0.515	38.89	220	9	4.1%	0.017	0.530	34.05
Region												
N Pacific	216	2	0.9%	0.039	0.444	42.53	216	2	0.9%	0.034	0.450	39.89
North GOA	80	15	18.8%	0.014	0.531	37.33	80	19	23.8%	0.023	0.515	34.01
PWS	80	11	13.8%	0.036	0.595	20.00	80	8	10.0%	0.049	0.583	18.73
PWS Entrance	184	8	4.3%	0.030	0.849	**4.51**	184	4	2.2%	0.069	0.722	10.25
Central PWS	80	9	11.3%	0.056	0.621	14.59	80	5	6.3%	0.032	0.686	13.46
Montague Strait	80	7	8.8%	0.036	0.738	**7.71**	80	5	6.3%	0.046	0.659	9.92
Northeast PWS	80	8	10.0%	0.041	0.961	**1.96**	80	4	5.0%	0.038	0.957	**0.96**
North Shore	80	9	11.3%	0.037	0.789	**7.50**	80	4	5.0%	0.016	0.867	**5.64**
Southeast PWS	80	7	8.8%	0.059	0.687	14.30	80	7	8.8%	0.053	0.765	**7.39**
Southwest PWS	80	7	8.8%	0.046	0.659	10.22	80	4	5.0%	0.036	0.654	10.96
Lag												
-1	249	18	7.2%	0.048	0.750	**8.97**	249	11	4.4%	0.058	0.678	**10.64**
0	249	14	5.6%	0.026	0.740	14.12	249	20	8.0%	0.031	0.638	21.80
1	249	29	11.6%	0.039	0.697	14.04	249	18	7.2%	0.032	0.661	16.17
2	249	13	5.2%	0.043	0.648	20.21	249	9	3.6%	0.037	0.691	18.03
Type												
Age3 - Local and Soundwide	-	0	-	-	-	-	5	4	80.0%	0.001	0.702	27.91
Spawn - Local and Soundwide	4	0	0.0%	-	-	-	4	1	25.0%	0.054	0.392	42.38
Fishing Mortality - Soundwide	1	0	0.0%	-	-	-	1	0	0.0%	-	-	-
Climate - Soundwide	36	2	5.6%	0.039	0.444	42.53	36	2	5.6%	0.034	0.450	39.89
Precip. and Air Temp. - Soundwide	96	0	0.0%	-	-	-	96	0	0.0%	-	-	-
Fresh Water - Soundwide	48	2	4.2%	0.009	0.508	39.38	48	0	0.0%	-	-	-
Upwelling - Soundwide	48	8	16.7%	0.028	0.479	39.72	48	4	8.3%	0.022	0.494	36.80
Mean Wind - Soundwide	24	4	16.7%	0.014	0.546	36.13	24	7	29.2%	0.019	0.547	32.34
Wind Mixing - Soundwide	24	0	0.0%	-	-	-	24	1	4.2%	0.019	0.508	35.98
Var. Wind - Soundwide	24	1	4.2%	0.004	0.603	30.32	24	4	16.7%	0.032	0.479	31.91
Wind Events - Soundwide	24	2	8.3%	0.007	0.583	34.32	24	4	16.7%	0.027	0.501	36.31
Zooplankton - Soundwide	8	2	25.0%	0.005	0.669	19.68	8	1	12.5%	0.013	0.604	20.71
Salinity - Local and Soundwide	160	13	8.1%	0.053	0.696	**9.99**	160	9	5.6%	0.043	0.786	**6.25**
Temperature - Local and Soundwide	160	24	15.0%	0.040	0.720	10.50	160	13	8.1%	0.052	0.672	12.96
Var. Salinity - Local and Soundwide	160	9	5.6%	0.028	0.804	**7.87**	160	6	3.8%	0.044	0.738	**7.31**
Var. Temp. - Local and Soundwide	160	16	10.0%	0.050	0.785	**7.74**	160	11	6.9%	0.038	0.750	**9.47**
Grand Total	**977**	**74**	**7.6%**	**0.039**	**0.709**	**13.91**	**982**	**58**	**5.9%**	**0.037**	**0.661**	**17.90**

Table 3.3. Log-transformed (ln) PWS total recruit-per-spawner (R/S) age-3 models with a spawn index variable were compared to environmental recruitment models for general additive models (gam) and linear models (lm). Three of the best-fitting environmental parameters shown were used for hypothesis testing. Model statistics shown are: gam residual deviance (D) and its lm equivalent, residual sum of squares (RSS); the square root of the gam dispersion parameter (ϕ) and its lm equivalent, residual standard error (RSE); the coefficient of determination or multiple determination (R^2); the number of data points in the model (N); the F statistic; the p-value, the Akaike Information Criteria (AIC); and the ANOVA test results, used to test hypotheses. Also shown are the regression statistics including the model coefficients and its standard error (SE), F statistic and p-value. The Principal Components wind variable (PC1 Wind) is defined in Appendix II.

Regression Parameters and Model Type		Model Statistics								Regression Statistics			
Response: Ln Age 3 Recruitment/Spawn Model No.		GAM: D or LM: RSS	GAM: Sqrt(ϕ) or LM: RSE	Multiple R^2	N	df	F	p-value	AIC	Coeff.	SE	GAM: NP F or LM: F	p-value
1 GAM:	Recruitment on Total Spawn	44.529	1.3344	0.339	24	19			47.20				
	Spline Fit: Total Spawn											1.869	0.1691
2 LM:	Recruitment on Total Spawn	46.565	1.4890	0.203	24	21	2.667	0.0929	23.00				
	Intercept									3.190	0.304	10.481	0.0000
	Polynomial, 2 df Fit: Total Spawn, coeff.1									-0.876	1.509	-0.581	0.5676
	coeff.2									3.363	1.502	2.238	0.0362
3 GAM:	Recruitment on Total Spawn and SSS	2.478	0.7040	0.821	11	5			4.46				
	Spline Fit: Total Spawn											0.804	0.5431
	Linear Fit: PWS July-Aug. Salinity Lag -1												
Test	**ANOVA; model 3 vs 1; 3 sig. better**						**6.06**	**0.0290**					
4 LM:	Recruitment on Total Spawn and SSS	3.672	0.6775	0.734	11	8		0.0137	12.00				
	Intercept									4.851	0.496	9.786	0.0000
	Linear Fit: Total Spawn									-0.024	0.007	-3.339	0.0102
	Linear Fit: PWS July-Aug. Salinity Lag -1									-0.550	0.164	-3.362	0.0099
Test	**ANOVA; model 4 vs 2; 4 sig. better**						**7.189**	**0.0044**					
5 LM:	Recruitment on Total Spawn and SSS	3.279	0.6844	0.763	11	7	7.501	0.0137	11.00				
	Intercept									3.335	0.218	15.336	0.0000
	Poly., 2 Fit: Total Spawn, coeff.1									-6.164	2.726	-2.261	0.0582
	coeff.2									-2.608	2.848	-0.916	0.3903
	Linear Fit: PWS July-Aug. Salinity Lag -1									-0.512	0.171	-3.006	0.0198
Test	**ANOVA; model 5 vs 4, ns; 5 vs 2; 4 sig. Better**						**6.600**	**0.0090**					
6 GAM:	Recruitment on Zooplankton and SSS	1.120	0.6110	0.912	9	3			2.61				
	Spline Fit: Zooplankton Lag +1											2.308	0.2549
	Linear Fit: PWS July-Aug. Salinity Lag -1												
7 LM:	Recruitment on Zooplankton and SSS	3.705	0.7858	0.709	9	6	7.309	0.0246	10.00				
	Intercept									3.179	0.340	9.359	0.0010
	Linear Fit: Zooplankton Lag +1									0.721	0.475	1.516	0.1802
	Linear Fit: PWS July-Aug. Salinity Lag -1									-0.874	0.308	-2.840	0.0296
8 LM:	Recruitment on Zooplankton and SSS	2.242	0.6696	0.824	9	5	7.798	0.0248	9.00				
	Intercept									1.726	0.855	2.202	0.0994
	Poly., 2 Fit: Zooplankton Lag +1, coeff.1									-12.093	8.950	-1.351	0.2346
	coeff.2									-9.372	5.188	-1.806	0.1307
	Linear Fit: PWS July-Aug. Salinity Lag -1									-0.860	0.263	-3.278	0.0220
9 GAM:	Recruitment on Wind and SSS	0.939	0.6853	0.910	9	2			2.82				
	Spline Fit: PC1 of Mean Wind											1.175	0.4904
	Linear Fit: PWS July-Aug. Salinity Lag -1												
10 LM:	Recruitment on Wind and SSS	2.595	0.7204	0.752	8	5	7.564	0.0308	9.00				
	Intercept									5.505	0.874	6.302	0.0015
	Linear Fit: PC1 of Mean Wind									-1.022	0.375	-2.724	0.0416
	Linear Fit: PWS July-Aug. Salinity Lag -1									-0.074	0.025	-2.947	0.0320
11 LM:	Recruitment on Wind and SSS	1.731	0.6579	0.834	8	4	6.713	0.0486	8.00				
	Intercept									2.730	0.331	8.258	0.0012
	Poly., 2 Fit: PC1 of Mean Wind, coeff.1									-7.943	3.083	-2.576	0.0616
	coeff.2									-3.901	2.761	-1.413	0.2306
	Linear Fit: PWS July-Aug. Salinity Lag -1									-1.001	0.343	-2.919	0.0433

Table 3.4. The log-transformed PWS recruit-per-spawner age 4 models with a spawn variable are compared with models containing age-3 recruitment variables and/or environmental parameters.

Regression Parameters and Model Type	Model Statistics								Regression Statistics			
Response: Ln Age 4 Recruitment/Spawn Model No.	GAM: D or LM: RSS	GAM: Sqrt(ϕ) or LM: RSE	Multiple R^2	N	df	F	p-value	AIC	Coeff.	SE	GAM: NP F or LM: F	p-value
1 GAM. Recruitment on Montague Spawn	28.167	1.2510	0.384	23	18			31.30				
Spline Fit: MT Spawn											3.403	0.0402
2 LM. Recruitment on Montague Spawn	31.814	1.2610	0.304	23	20	4.373	0.0266	22.01				
Intercept									4.019	0.265	15.183	0.0000
Poly., 2 Fit: MT Spawn, coeff.1									-1.434	1.281	-1.119	0.2763
coeff.2									3.707	1.331	2.785	0.0114
Test ANOVA; model 1 vs w/Total Spawn; MT spawn sig. better						**3675.09**	**0.0000**					
Test ANOVA; N spawn vs Total Spawn; N spawn sig.better fit						**338.64**	**0.0001**					
3 LM. Recruitment on Eastern Age 3 Recruitment	21.809	1.0190	0.523	23	21	23.030	0.0001	23.00				
Intercept									0.028	0.876	0.032	0.9752
Linear Fit: E3									0.666	0.137	4.799	0.0001
Test ANOVA; model 3 vs 2; 3 sig. better						**5.892**	**0.0200**					
4 GAM. Recruitment on E. Age 3 Rec. & Montague Spawn	14.177	0.5816	0.690	22	17			14.85				
Linear Fit: E3												
Spline Fit: MT Spawn											2.923	0.0639
5 LM. Recruitment on E. Age 3 Rec. & Montague Spawn	17.278	0.9536	0.622	22	19	10.430	0.0003	23.00				
Intercept									0.648	0.867	0.748	0.4636
Linear Fit: E3									0.556	0.139	3.998	0.0008
Poly., 2 df Fit: MT Spawn, coeff.1									-0.783	0.983	-0.797	0.4354
coeff.2									2.296	1.067	2.152	0.0444
Test ANOVA; model 5 vs 3; ns												
6 GAM. Recruitment on E. Age 3 Rec. & SSS	3.391	0.7519	0.888	22	6			5.65				
Spline Fit: PWS Sept.-Oct. Salinity Lag -1											3.622	0.0847
7 LM. Recruitment on E. Age 3 Rec. & SSS	9.519	1.0280	0.684	22	9	9.757	0.0056	13.01				
Intercept									-0.437	1.468	-0.298	0.7727
Linear Fit: E3									0.783	0.232	3.368	0.0083
Linear Fit: PWS Sept.-Oct. Salinity Lag -1									-0.098	0.413	-0.237	0.8181
8 LM. Recruitment on E. Age 3 Rec.& SSS	8.681	1.0420	0.712	22	8	6.598	0.0148	12.00				
Intercept									-1.122	1.679	-0.668	0.5227
Linear Fit: E3									0.870	0.256	3.405	0.0093
Poly., 2 Fit: PWS Sept.-Oct. Sal. Lag -1, coeff.1									0.538	2.081	0.259	0.8024
coeff.2									-2.335	2.657	-0.879	0.4050
9 LM. Recruitment on E. Age 3 Rec. & Wind Speed	14.906	0.9100	0.661	22	18	17.510	0.0001	22.00				
Intercept									1.885	1.105	1.706	0.1053
Linear Fit: E3									0.493	0.143	3.438	0.0029
Linear Fit: Mean Wind Speed, Jan.-Feb. Lag 0									0.391	0.158	2.468	0.0238
10 GAM. Recruitment on Zooplankton & Wind Speed	6.834	0.9242	0.741	17	8			10.25				
Spline Fit:Average Zoop. Settled Volume Lag +1											0.882	0.4900
Linear Fit: Mean Wind Speed, Jan.-Feb. Lag 0											-	-
11 LM. Recruitment on Zooplankton & Wind Speed	9.095	0.9093	0.655	17	11	10.440	0.0029	15.00				
Intercept									5.707	0.734	7.772	0.0000
Linear Fit: Ave. Zooplankton Settled Volume Lag +1									0.620	0.186	3.334	0.0067
Linear Fit: Mean Wind Speed, Jan.-Feb. Lag 0									0.712	0.247	2.876	0.0151
12 LM. Recruitment on Zooplankton & Wind Speed	7.223	0.8499	0.726	17	10	8.831	0.0037	12.00				
Intercept									4.247	0.301	14.093	0.0000
Linear Fit: Ave. Zooplankton Settled Volume Lag +1									0.708	0.182	3.883	0.0030
Poly., 2 Fit: Mean W.S., Jan.-Feb. Lag 0, coeff.1									6.201	1.856	3.342	0.0075
coeff.2									3.230	2.006	1.610	0.1384

Table 3.5. Significant correlations ($\alpha \leq 0.10$) among herring variables are shown along with correlation coefficients (r) and significance level (p-value). Recruitment variables include Eastern age-3 or -4 (E3 or 4), Northern (N3 or 4), Montague (MT3 or 4), PWS total recruitment (PWS Tot 3 or 4); and PWS total recruit-per-spawner (R/S) ratios. Spawn index variables include the same regions and are denoted with SPN; ln denotes log-transformations.

Correlation Type	Variable 1	Variable 2	r	p-value
Correlation among spawn index variables	ESPN	PWS SPN	0.647	<0.0005
	NSPN	PWS SPN	0.685	<0.0005
	MTSPN	PWS SPN	0.723	<0.0005
	lnESPN	lnPWS SPN	0.616	0.001
	lnNSPN	lnPWS SPN	0.767	<0.0005
	lnMTSPN	lnPWS SPN	0.500	0.008
Correlation among age-3 recruitment variables	lnE3	lnN3	0.515	0.010
	E3	PWSTot3	0.766	<0.0005
	MT3	PWSTot3	0.611	0.002
	lnE3	lnPWSTot 3	0.844	<0.0005
	lnN3	lnPWSTot 3	0.511	0.011
	lnMT3	lnPWSTot 3	0.711	<0.0005
	lnE3	lnPWS R/S 3	0.863	<0.0005
	lnMT3	lnPWS R/S 3	0.538	0.008
Correlation among age-4 recruitment variables	lnE4	lnN4	0.510	0.013
	E4	MT4	0.553	0.006
	N4	MT4	0.713	<0.0005
	E4	PWSTot 4	0.818	<0.0005
	N4	PWSTot 4	0.617	0.002
	MT4	PWSTot 4	0.922	<0.0005
	lnE4	lnPWSTot 4	0.885	<0.0005
	lnN4	lnPWSTot 4	0.486	0.019
	lnMT4	lnPWSTot 4	0.697	<0.0005
	lnE4	lnPWS R/S 4	0.910	<0.0005
	lnN4	lnPWS R/S 4	0.444	0.034
	lnMT4	lnPWS R/S 4	0.573	0.004
Correlation between age-3 and age-4 recruitment variables	E3	E4	0.932	<0.0005
	lnE3	lnE4	0.699	<0.0005
	E3	MT4	0.368	0.084
	lnE3	lnMT4	0.368	0.085
	N3	N4	0.864	<0.0005
	lnN3	lnN4	0.625	0.001
	N3	MT4	0.585	0.003
	MT3	MT4	0.454	0.03
	lnMT3	lnMT4	0.684	<0.0005
	E3	PWSTot 4	0.656	0.001
	N3	PWSTot 4	0.497	0.016
	lnE3	lnPWSTot 4	0.687	<0.0005
	lnE3	lnPWS R/S 4	0.723	<0.0005
	lnPWS R\S 3	lnPWS R/S 4	0.751	<0.0005

Table 3.6. Significant correlations ($\alpha \leq 0.10$) between recruitment and spawn index variables; the correlation coefficients (r) and level of significance (p-value) are shown. Recruitment variables include Eastern age3 or 4 (E3 or 4), Northern (N3 or 4), Montague (MT3 or 4), PWS total recruitment (PWS Tot 3 or 4); and PWS total recruit-per-spawner (R/S) ratios. Spawn index variables include the same regions and are denoted with SPN; ln denotes log-transformations.

Type	Recruitment	Spawn	r	p-value
Correlations between Age-3 recruitment and spawn index	MT3	E SPN	0.452	0.027
	MT3	MT SPN	0.702	<0.0005
	MT3	PWS SPN	0.660	<0.0005
	ln MT3	MT SPN	0.436	0.033
	ln MT3	PWS SPN	0.403	0.051
	ln PWS R/S 3	ln N SPN	-0.409	0.053
	ln PWS R/S 3	N SPN	-0.398	0.060
Correlations between Age-4 recruitment and spawn index	ln E4	ln MT SPN	-0.376	0.077
	ln MT4	ln E SPN	0.369	0.083
	ln PWS Tot 4	ln E SPN	0.357	0.011
	ln PWS R/S 4	ln MT SPN	-0.407	0.054
	ln PWS R/S 4	ln N SPN	-0.394	0.063
	ln PWS R/S 4	N SPN	-0.358	0.094

Table 3.7. The average AIC, under each recruitment variable (Eastern age-3 and –4 recruitment, E3 & 4; Northern, N3 & 4; Montague, MT3 & 4; PWS total. TOT3 & 4; PWS recruit-per-spawner ratios, LNR/S3 & 4) for environmental variables categorized by season and lag, the average AIC for each temporal category over all recruitment variables, and the percentage of significant variables (V) for each category (highest values bolded) out of the total number of variables (Total V) possible. The AIC values lower than 10 are highlighted and the lowest AIC in each category are bolded.

	Lag	E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Average AIC by Category	% Total V Possible	Total V Possible
Annual	**-1**											-	0.0%	50
	0			73.98								73.98	2.0%	50
	1											-	0.0%	50
	2		146.12									146.12	2.0%	50
Annual Total		30.65	103.89	73.98	26.98	19.68	19.89	84.41		19.86	20.71	56.93	**1.0%**	200
Spring	**-1**	160.03	**7.41**	24.68	**5.64**	13.33	11.57	48.56	87.40	10.13	**5.75**	36.91	12.0%	450
	0	43.65	23.95	**7.20**		49.66	25.51	94.15	51.35	**9.58**	**8.56**	40.13	4.7%	450
	1	**23.14**	24.50	18.56	20.56	27.51	39.76	61.36	75.94	20.55	18.92	29.26	12.7%	450
	2	117.90	27.87	15.03	16.76	26.57	14.66	31.74	41.22	15.84	17.21	32.60	7.1%	450
Spring Total		76.62	20.32	17.53	15.76	27.19	20.62	53.64	65.28	14.72	12.85	33.57	**9.1%**	1800
Early Summer	**-1**	141.91	62.10	25.94	16.43		13.49	58.12	20.72	**9.39**		47.34	6.8%	500
	0	83.72	58.03	17.49	27.41	16.91	21.04	55.00	19.82	10.67	**9.96**	32.09	6.0%	500
	1		53.67	52.24	21.69	11.14	11.30	49.90	24.09	**8.12**	**9.02**	24.67	5.2%	500
	2	119.43	49.30	**9.35**	11.65	23.94	34.34	41.65	26.79	24.90	24.27	48.33	9.0%	500
Early Summer Total		121.07	54.13	26.15	17.82	18.98	20.83	48.07	22.49	10.50	14.97	39.91	6.8%	2000
Late Summer	**-1**	60.87	**9.63**	14.36	**3.43**	**5.35**	**3.44**	36.37	10.86	**2.65**	**5.40**	**12.59**	11.1%	460
	0	64.67	11.20	30.03	12.62	12.66	13.01	21.94	22.87	14.18	19.69	21.89	16.1%	460
	1			15.50	**2.38**	**1.05**	**3.15**	**8.15**	10.73	**7.33**	**2.36**	**8.86**	7.8%	460
	2	260.40		36.87	**4.93**	**6.64**	**6.63**	50.47		**2.58**	**3.45**	65.43	2.4%	460
Late Summer Total		103.44	10.29	19.63	7.57	6.95	6.82	29.65	18.32	10.09	14.26	19.14	9.2%	1840
Fall	**-1**	96.08	44.67	31.25	16.75	**9.77**	17.65	44.07	**2.31**	**9.43**	15.71	33.99	11.7%	480
	0	166.35	66.35	23.40	12.53	20.28	13.73	34.89	**5.34**	35.59	17.20	40.73	5.8%	480
	1	189.03	32.24	35.96	13.35	12.80	**7.18**	53.88	25.40	**6.95**	9.40	29.55	12.9%	480
	2		46.61	10.91	20.42	18.24	19.15		28.58		11.25	19.86	5.0%	480
Fall Total		126.68	45.67	26.62	15.23	14.06	14.44	41.88	21.70	13.42	14.25	31.49	8.9%	1920
Winter	**-1**		137.90	68.93				137.97				130.28	1.6%	550
	0	45.09					38.88	148.26	78.19	32.57	33.31	47.20	3.8%	550
	1	161.85	130.80			35.80	41.18				39.93	96.65	1.5%	550
	2	388.12	131.03		51.78	39.03	38.13	147.73		30.01	33.48	102.85	1.8%	550
Winter Total		160.64	133.73	68.93	51.78	37.41	38.99	140.48	78.19	32.14	34.80	82.61	2.2%	2200
Average by Recruit. Var.		**108.39**	**51.97**	**25.68**	**13.69**	**13.91**	**18.54**	**57.14**	**23.15**	**13.47**	**17.90**	**Overall Average**		**34.38**
Total No. Sig. Variables		**73**	**59**	**90**	**81**	**74**	**63**	**71**	**73**	**63**	**58**	**705**	**7.1%**	**9960**

Table 3.8. The average AIC, under each recruitment variable (Eastern age-3 and –4 recruitment, E3 & 4; Northern, N3 & 4; Montague, MT3 & 4; PWS total. TOT3 & 4; PWS recruit-per-spawner ratios, LNR/S3 & 4) for environmental variables categorized by the environmental forcing location, only for Spring through Fall seasons over all lags, the average AIC for each category over all recruitment variables, and the percentage of significant variables (V) for each category (highest values bolded) out of the total number of variables (Total V) possible. The AIC values lower than 10 are highlighted and the lowest AIC in each category are bolded.

	E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Average by Region	% of Total Possible	Total No. Variables Possible
North Pacific					42.53		147.79		36.17	41.37	86.57	5.8%	120
North GOA	172.41	127.33	71.46	41.53	38.24	35.05		60.30	31.91	34.36	67.76	3.5%	1520
PWS	76.84	26.16	20.00	18.73	34.34	32.81	78.30	78.05	20.71	17.68	42.75	7.4%	1440
PWS Entrance	**19.52**	21.09	19.48	**6.23**	**4.51**	10.31	21.99	13.24	**5.59**	10.25	**13.42**	8.9%	640
Central PWS	113.54	44.57	21.91	12.72	14.59	16.46	44.99	21.43	11.24	13.46	30.42	10.6%	640
Montague Strait	107.15	36.30	24.67	11.81	**7.71**	12.34	46.12	11.43	**8.25**	**9.92**	29.72	**12.3%**	640
Northeast PWS	106.33	**3.46**	**4.78**	**1.95**	**1.96**	**7.27**	**8.30**	**4.77**	**0.66**	**0.96**	18.78	9.5%	640
North Shore	128.06	27.45	14.08	**9.40**	**7.50**	**7.38**	23.29	17.33	**5.25**	**5.64**	24.56	**12.3%**	640
Southeast PWS	58.56	12.15	**8.26**	**5.57**	**5.49**	**4.29**	20.07	**8.94**	**4.75**	**3.60**	**13.51**	**12.2%**	640
Southwest PWS	91.02	55.97	40.06	16.56	12.54	19.95	43.03	24.25	11.14	13.31	29.71	10.3%	640
Average by Recruit. Variable	**106.11**	**38.32**	**24.64**	**12.86**	**13.07**	**15.83**	**44.67**	**20.79**	**11.35**	**14.68**	**30.08**	**8.4%**	**7560**

Table 3.9. The average AIC, under each recruitment variable (Eastern age-3 and –4 recruitment, E3 & 4; Northern, N3 & 4; Montague, MT3 & 4; PWS total. TOT3 & 4; PWS recruit-per-spawner ratios, LNR/S3 & 4) for environmental variables categorized by type, only for Spring through Fall seasons over all lags, the average AIC for each category over all recruitment variables, and the percentage of significant variables (V) for each category (highest values bolded) out of the total number of variables (Total V) possible. The AIC values lower than 10 are highlighted and the lowest AIC in each category are bolded.

	E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Average by Region	% of Total Possible	Total No. Variables Possible
Climate					42.53		147.79		36.17	41.37	86.57	5.8%	120
Freshwater	385.41		71.20	48.60	40.17			71.80			114.73	0.0%	360
Upwelling	313.05	127.33			42.79	42.38			35.59	39.72	122.52	3.1%	360
Mean Wind	44.17				35.13	33.07			24.90	31.62	35.90	7.5%	160
Wind Mixing			71.66	44.85		36.50		71.50		33.81	57.35	4.4%	160
Var. Wind	50.45		75.51	38.26	33.51	27.00		43.99	33.06	34.28	44.59	6.3%	160
Wind Events			63.46	34.38	35.05	32.96		42.71	30.38	37.94	35.35	1.9%	320
Zooplankton	**30.65**	93.33		26.98	19.68	19.89	84.41		19.86	20.71	50.68	**21.3%**	80
Salinity	46.69	41.69	20.97	12.91	11.47	**9.19**	**41.48**	16.91	**9.32**	**6.45**	**21.39**	10.3%	1280
Temperature	51.60	**26.79**	**18.45**	10.50	10.77	14.11	42.67	20.40	**8.89**	13.16	**21.68**	12.3%	1280
Var. Salinity	192.36	26.85	22.28	**9.91**	**7.31**	12.35	25.53	23.40	**6.15**	**7.78**	41.37	9.2%	1280
Var. Temp.	64.25	40.49	19.89	12.24	**8.35**	12.66	41.97	**13.58**	**9.85**	10.47	22.72	13.4%	1280
Average by Recruit. Variable	**103.85**	**42.48**	**24.64**	**13.21**	**13.25**	**15.98**	**46.56**	**20.79**	**11.50**	**14.80**	**30.62**	**8.6%**	**7560**

Table 3.10. Shown here are only the average AIC for combinations of seasons, lag, local forcing region, and type of variable with the lowest values (highlighted and bolded) for at least one of the recruitment variables. The + or – symbols represent the sign of the functional relationship between the recruitment and environmental variable. The categorical AIC average is also shown with the lowest values bolded.

Season	Lag	Local Region	Type	E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Categorical Average
Spring	1	SE	S	**2.39 +**	20.54 +			11.74 +	7.77 +	39.69 +		9.20 +	5.39 +	13.82
		NE	T						**0.15 +**			**0.01 +**		**0.08**
	-1	NE	VS		**0.01 -**		**0.00 -**	**0.01 -**		**2.68 -**				0.67
		NE	VT		0.22 -		**0.04 -**	**0.10 -**						0.12
Late Summer	0	NE	T	158.18 +		**0.01 -**	**0.04 +**							52.74
	1	SE	S						4.47 +		0.47 +	0.56 +	**0.12 +**	1.40
		NE	T					**0.04 -**						**0.04**
	2	SE	VT			**0.08 -**								**0.08**
		NE	VS	398.98 -		**0.05 -**	**0.09 -**	**0.09 -**						99.80
	-1	NE	VT		**0.01 +**						**0.04 -**			**0.02**
Fall		SE	VT						**0.26 -**	7.16 -			1.34 -	2.92
	0	NE	S			**0.00 +**		**0.01 -**	15.40 -				0.21 -	3.91
	2	NE	S										**0.10 +**	0.10

Table 3.11. Expanded list of significant variables (salinity, S; SST, T; variance in salinity, VS; variance in SST, VT; freshwater flow, FW; mean wind speed, MW; wind mixing, MW3; variance in mean wind speed, VW; gail force wind events, GFWE; high speed wind events, HSWE; upwelling index, UW; climate indices, CLIM; zooplankton, Z) and the average AIC scores for those variables correlated to each recruitment variable (variable (Eastern age-3 and –4 recruitment, E3 & 4; Northern, N3 & 4; Montague, MT3 & 4; PWS total, TOT3 & 4; PWS recruit-per-spawner ratios, LNR/S3 & 4) for the eight critical periods identified by model results. The highest AIC score in each period for each recruitment variable is bolded and values under 10 are also highlighted. Critical life history periods with no significant variables under a particular recruitment variable are marked with an X.

			E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Categorical Average
1. Spring +1 lag	PWS	Z	30.65 +	92.51 +		**26.98 +**	**19.68 +**	19.89 +	86.74 +		19.86 +	20.71 +	42.39
	NGOA	MW	36.28 +									**37.00 +**	36.64
		MW3								92.57 +			92.57
		UW						40.55 +					40.55
	NE	T	19.07 +				**4.22 +**					**2.65 +**	8.65
		VT			16.23 +								16.23
	NS	T	16.28 +			**11.94 +**	**9.27 +**						12.50
		S			30.49 -								30.49
	PWSENT	T	**10.51 +**										10.51
		VS							**16.54 +**		**4.36 +**		10.45
		VT			**14.61 -**					**13.41 -**			14.01
	SE	S	**2.39 +**	**20.54 +**			11.74 +	**7.77 +**	39.69 +		**9.20 +**	**5.39 +**	13.82
		T			34.95 +								34.95
2. Late Summer -1 lag	CS	S			10.47 -		**7.89 -**						9.18
		T				**5.32 +**	**7.35 +**						6.33
		VT				**6.21 -**	**9.29 -**						7.75
	MS	S	**60.87 -**			**2.77 -**	**5.21 -**					**5.40 -**	18.56
		T							24.95 +				24.95
		VT		39.25 +									39.25
	NE	T						**0.15 +**			**0.01 +**		0.08
		VS		**0.01 -**		**0.00 -**	**0.01 -**		**2.68 -**				0.67
		VT		**0.22 -**		**0.04 -**	**0.10 -**						0.12
	NS	S			**9.85 -**								9.85
		T		15.28 +				**3.29 +**	11.01 +		**3.88 +**		8.37
		VS							25.18 -				25.18
		VT		**1.78 -**				**5.64**	**5.18 -**				4.20
	PWS	S			16.19 -	**5.61 -**	10.74 -						10.85
		T			36.01 +								36.01
	PWSENT	S			**6.45 -**	**3.91 -**							5.18
		T		**9.92 +**	20.77 +	**2.24 +**	**2.01 +**						8.74
		VT					**4.04 -**		31.47 -				17.76
	SE	T			**0.75 +**								0.75
		VT		**0.98 +**									0.98
	SW	T				**4.75 +**	**6.86 +**	**4.69 +**	39.87 +				14.04
		VS								**10.86 -**	**4.07 -**		7.46
3. Late Summer 0 lag	CS	S								10.82 -	11.08 -		10.95
		T	**15.34 +**					13.53 +			**8.20 +**	12.82 +	12.47
		VT									12.59 -		12.59
	MS	T	23.73 +	32.13 +		**3.63 +**	**6.41 +**	**8.42 +**	41.28 +		**6.02 +**	12.88 +	16.81
		VS								22.06 -			22.06
		VT	119.15 -	15.27 -		**4.19 -**	**4.84 -**	11.83 -	24.69 -		11.06 -	14.66 -	25.71
	NE	T	158.18 +		**0.01 -**	**0.04 +**							52.74
	NGOA	HSWE			63.46 +	34.38 +	35.05 +			42.71 +	30.38 +	37.94 +	40.65
		MW3			68.79	44.85 +				50.43 +			54.69
		VW	50.45 +			38.26 +	33.51 +			43.99 +	33.06 +	37.07 +	39.39
	NS	S				**1.28 -**				13.25 -			7.27
		T	63.17 +	**4.96 +**		**1.06 +**			18.30 +				21.87
		VT				**2.00 -**			**3.47 -**				2.74
	PWS	S			15.39 -								15.39
		T	22.69 +			**6.10 +**				23.60 +	12.12 +	18.43 +	16.59
		VT						18.27 -			15.25 -	17.95 -	17.16
	PWSENT	S			**2.51 -**					**3.75 -**			3.13
		T					**1.42 +**			16.15 +			8.79
		VT					**2.05 -**					**5.80 -**	3.93
	SE	T								**1.92 +**	**2.08 +**		2.00
		VS		**2.32 +**									2.32
		VT		**1.30 +**									1.30
	SW	T				**3.00 +**	**5.35 +**						4.18

Table 3.11. Continued.

			E3	N3	MT3	TOT3	LNR/S3	E4	N4	MT4	TOT4	LNR/S4	Categorical Average
4. Late Summer +1 lag	CS	S								14.10 +	12.08 +		13.09
		VT			12.84 +					**9.71 +**			11.27
	NE	T					**0.04 -**						0.04
	NS	T			**4.90 -**		**1.33 -**						3.12
		VT			**4.21 +**								4.21
	PWSENT	VS							11.78 -				11.78
		VT			12.01 +	**3.97 +**							7.99
	SE	S						**4.47 +**		**0.47 +**	**0.56 +**	**0.12 +**	1.40
		VS			**0.51 +**	**0.28 +**	**0.21 +**	**4.68 +**	**8.72 +**				2.88
		VT			**3.21 +**	**2.88 +**	**2.62 +**	**0.30 +**	**3.93 +**		**4.19**		2.86
	SW	S			48.35 +								48.35
		T			**4.95 -**								4.95
		VS										**4.60 -**	4.60
		VT								**7.60 +**			7.60
5. Late Summer +2 lag	NS	VS				**4.93 -**	**6.64 -**	**6.63 -**			**2.58 -**	**3.45 -**	54.09
	SE	VT			**0.08 -**								0.08
6. Fall -1 lag	MS	S						**6.59 +**	32.56 +				19.57
		VT								**4.58 +**			4.58
	NE	VS	398.98 -		**0.05 -**	**0.09 -**	**0.09 -**						99.80
		VT		**0.01 +**						**0.04 -**			0.02
	NGOA	FW			74.22 +	48.60 +							61.41
		GFWE						32.96 +					32.96
		MW	39.84 +					30.91 +				31.39 +	34.05
		VW						27.00 +				31.49 +	29.24
	NS	S	33.86 +			12.02 +							22.94
		VS	206.06 -		19.49 -	10.39 -	**3.13 -**	**4.73 -**			**3.03 -**	**1.37 -**	35.46
		VT					**9.92 +**	**7.09 +**			**2.18 +**	**2.85 +**	5.51
	PWSENT	S	**13.19 +**			**6.99 +**							10.09
		VS					**4.03 -**						4.03
	SE	VT						**0.26 -**	**7.16 -**			**1.34 -**	2.92
7. Fall 0 lag	MS	S								**5.35 -**			5.35
		T	57.65 -			**6.04 -**							31.85
		VT								**5.33 -**			5.33
	NE	S			**0.00 +**		**0.01 -**	15.40 -				**0.21 -**	3.91
	NGOA	MW	**48.14 +**										48.14
		UW	393.27 -	127.33 -			44.14 -				35.59 -	39.72 -	112.61
	NS	T				19.01 -			**14.27 -**				16.64
	PWSENT	S			28.42 -								28.42
		T						**12.06 -**	17.87 +				14.96
		VS										**10.13 -**	10.13
	SE	VS		**5.37 +**									5.37
8. Fall +2 lag	MS	S		**30.29 +**									30.29
		VS					**9.82 -**						9.82
	NE	S										**0.10 +**	0.10
		VS						**19.15 -**					19.15
	NS	S			**8.87 -**								8.87
		T			**7.92 +**								7.92
		VS			**8.90 +**								8.90
		VT								**5.35 -**			5.35
	PWSENT	T			**5.49 +**					21.59 +			13.54
		VT			13.09 -								13.09
	SE	T					1.96 '+						1.96

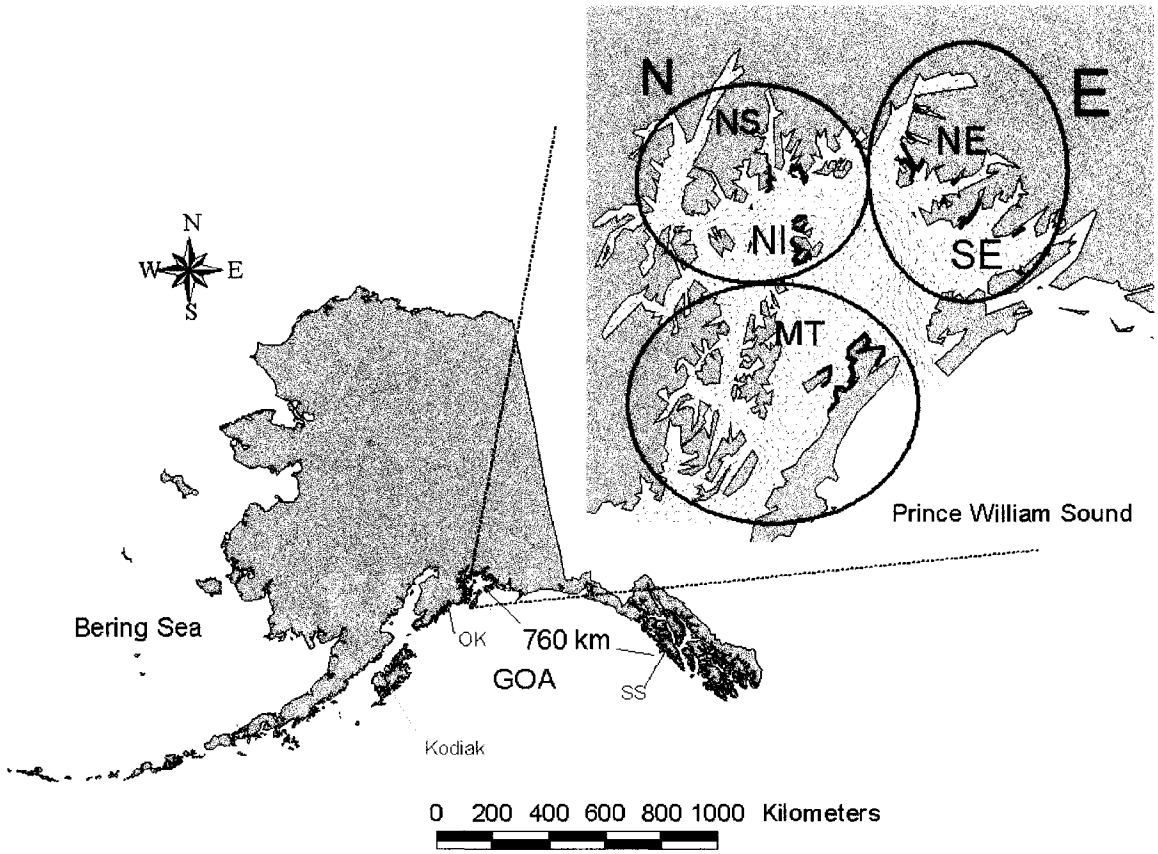


Figure 3.1. Locations of Prince William Sound (PWS), the Outer Kenai (OK), Sitka Sound (SS), Kodiak, and the Bering Sea in Alaska. The residual current structure during spawning (Moores and Wang, 1988; inset figure) and major spawning areas (darkened shorelines) in PWS include southeast (SE), northeast (NE), the north shore (NS), Naked Island (NI), and northern Montague Island (MT). Areas encircled represent the three hypothetical local populations (Chapter 2) and the pooling of spawning and recruiting areas into the Northern (N), Eastern (E), and Montague regions for the analysis.

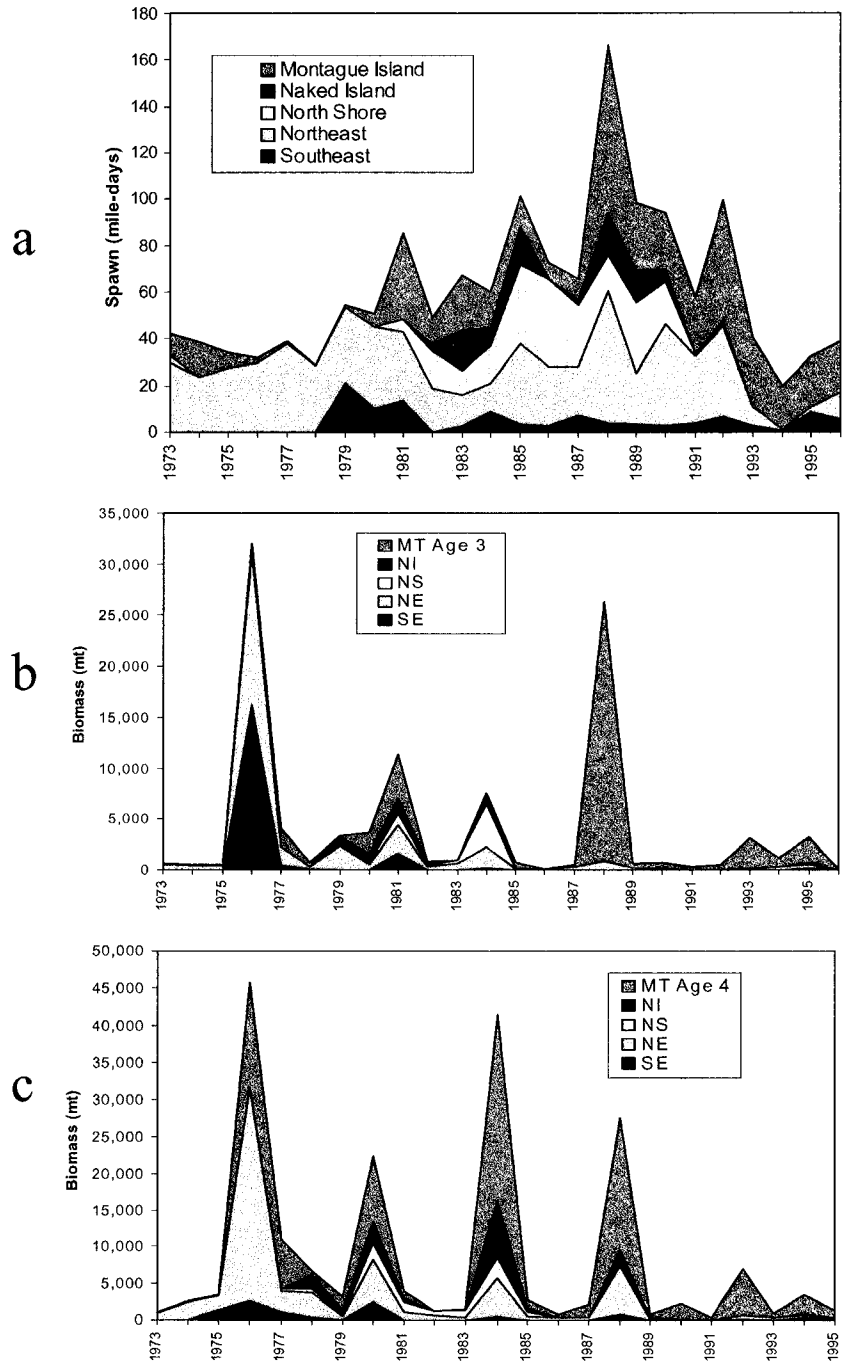


Figure 3.2. The **(a)** time series of spawn magnitude is expressed in mile-days and allocated by local region. Recruitment biomass to the adult spawning population in each of the same five regions is shown for **(b)** age-3 recruits and **(c)** age-4 recruits by the cohort year.

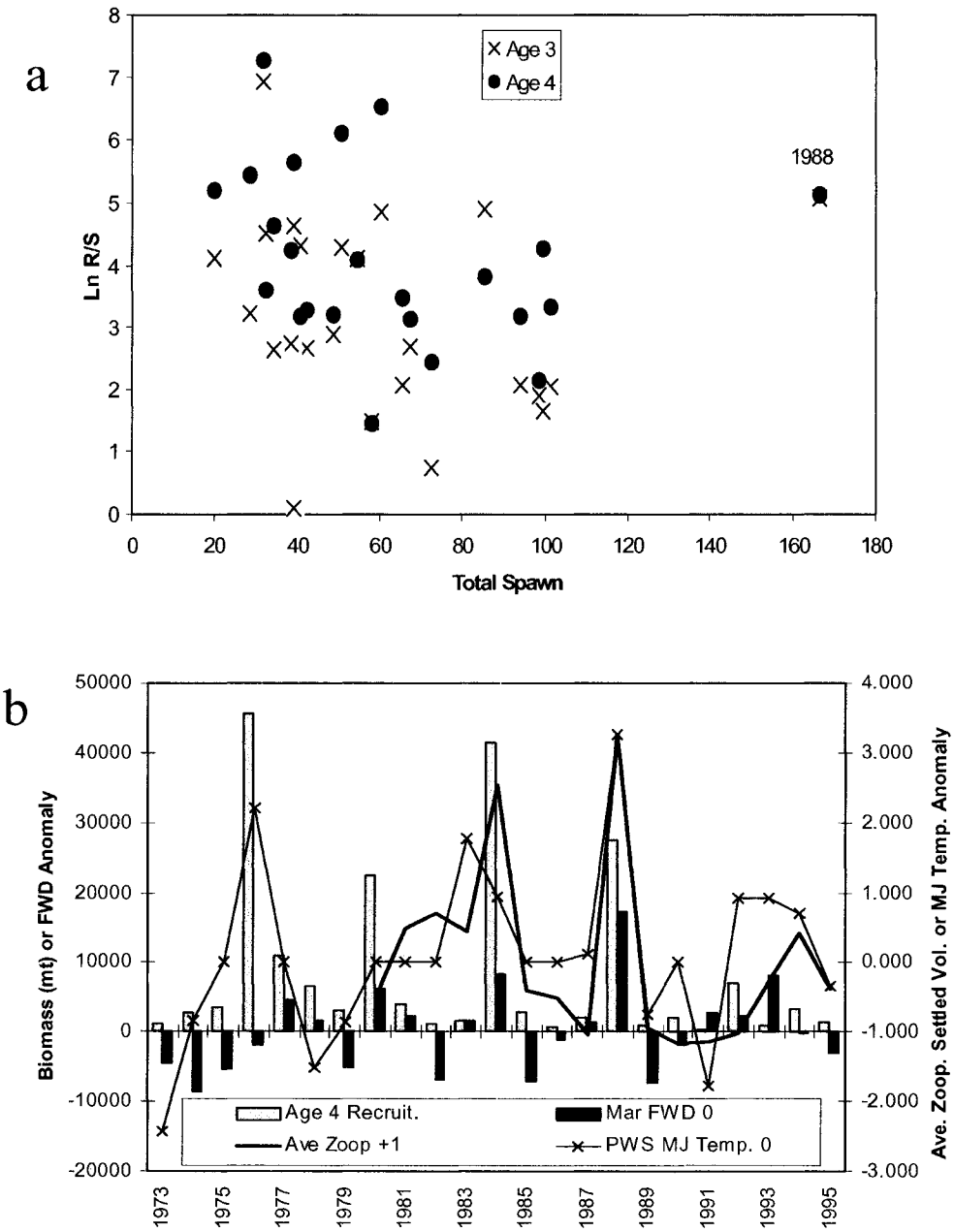


Figure 3.3. **(a)** Recruit-per-spawner (R/S) ratios, for age 3 and 4 recruits, plotted again the total spawn magnitude, in mile-days of spawn; the 1988 cohort is an extreme outlier. **(b)** Total age 4 recruiting biomass is shown with the March, freshwater discharge (Mar FWS) anomaly (Royer 1982) for the North Gulf of Alaska, the average zooplankton density anomaly, lagged a year ahead (Ave Zoop +1), and the average May-June upper 20m SST anomaly for PWS (PWS MJ Temp. 0).

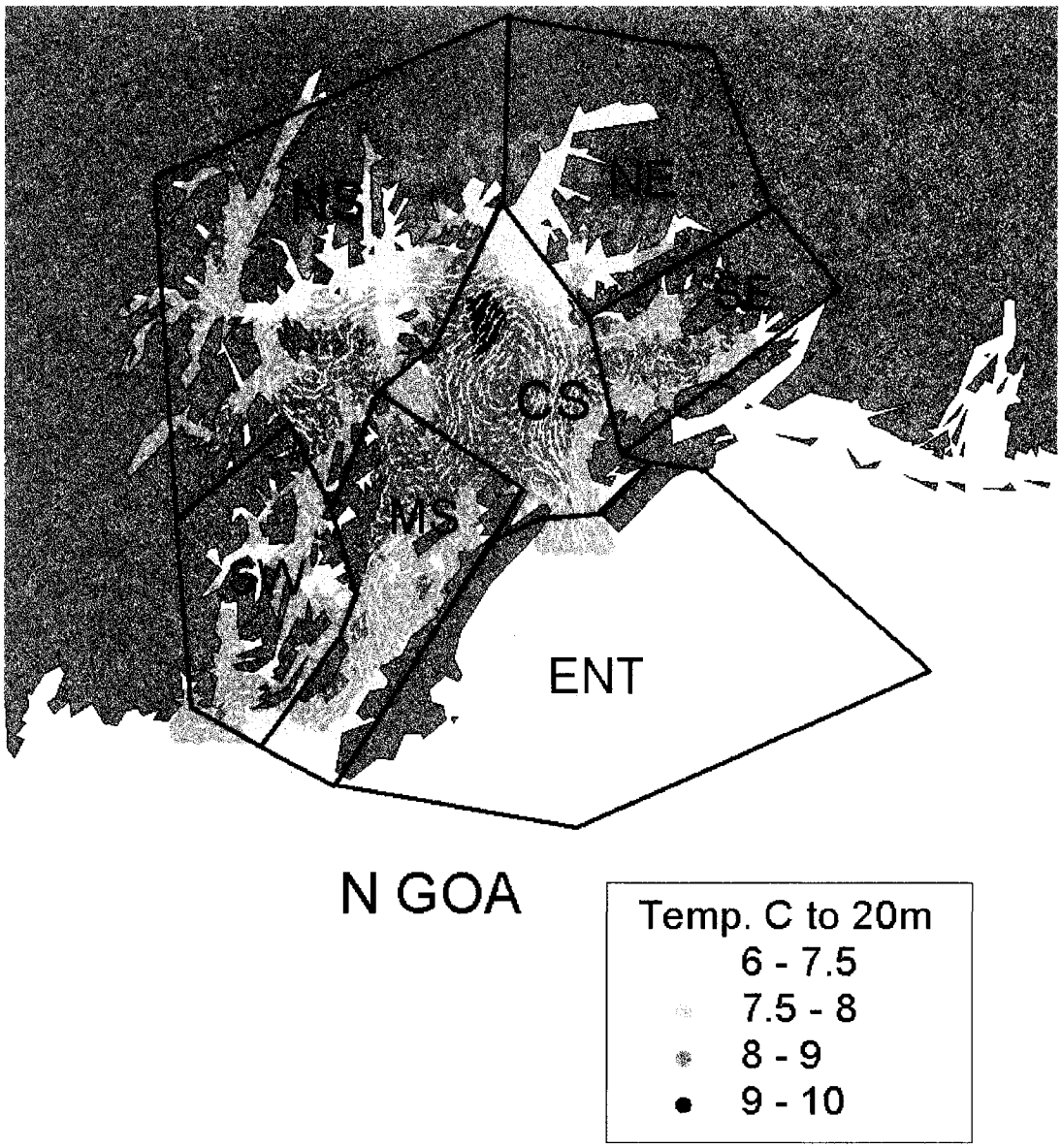


Figure 3.4. Oceanographic local regions within PWS are delineated over the modeled residual current in May (Wang et al. 1997, 2001) and a composite of May SST to 20 m from 1975 to 1990. The varying thermal structure is visible over Southeast (SE), Northeast (NE), North Shore (NS), Central Sound (CS), Montague Strait (MS), Southwestern (SW), and the Hinchinbrook entrance (ENT) to PWS.

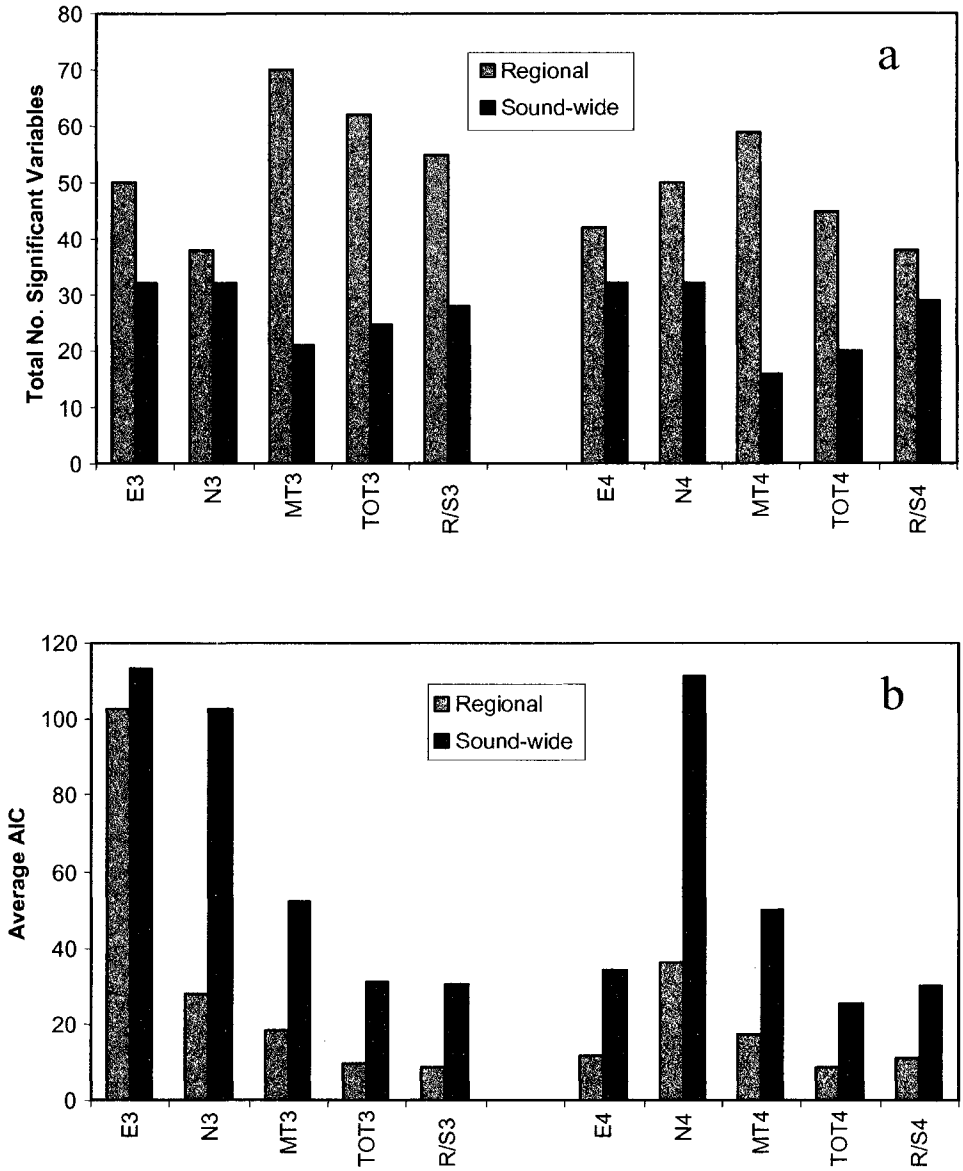


Figure 3.5. Allocation of significant environmental variables between those categorized as sound-wide forcing and PWS local forcing for **(a)** the log-transformed recruitment variables, Eastern age-3 and –4 recruitment (E3 & 4), Northern (N3 & 4), Montague (MT3 & 4), PWS total (TOT3 & 4), and the log-transformed PWS recruit-per-spawner ratios (R/S3 & 4; and **(b)** the average model Akaike Information Criteria (AIC; goodness of model fit).

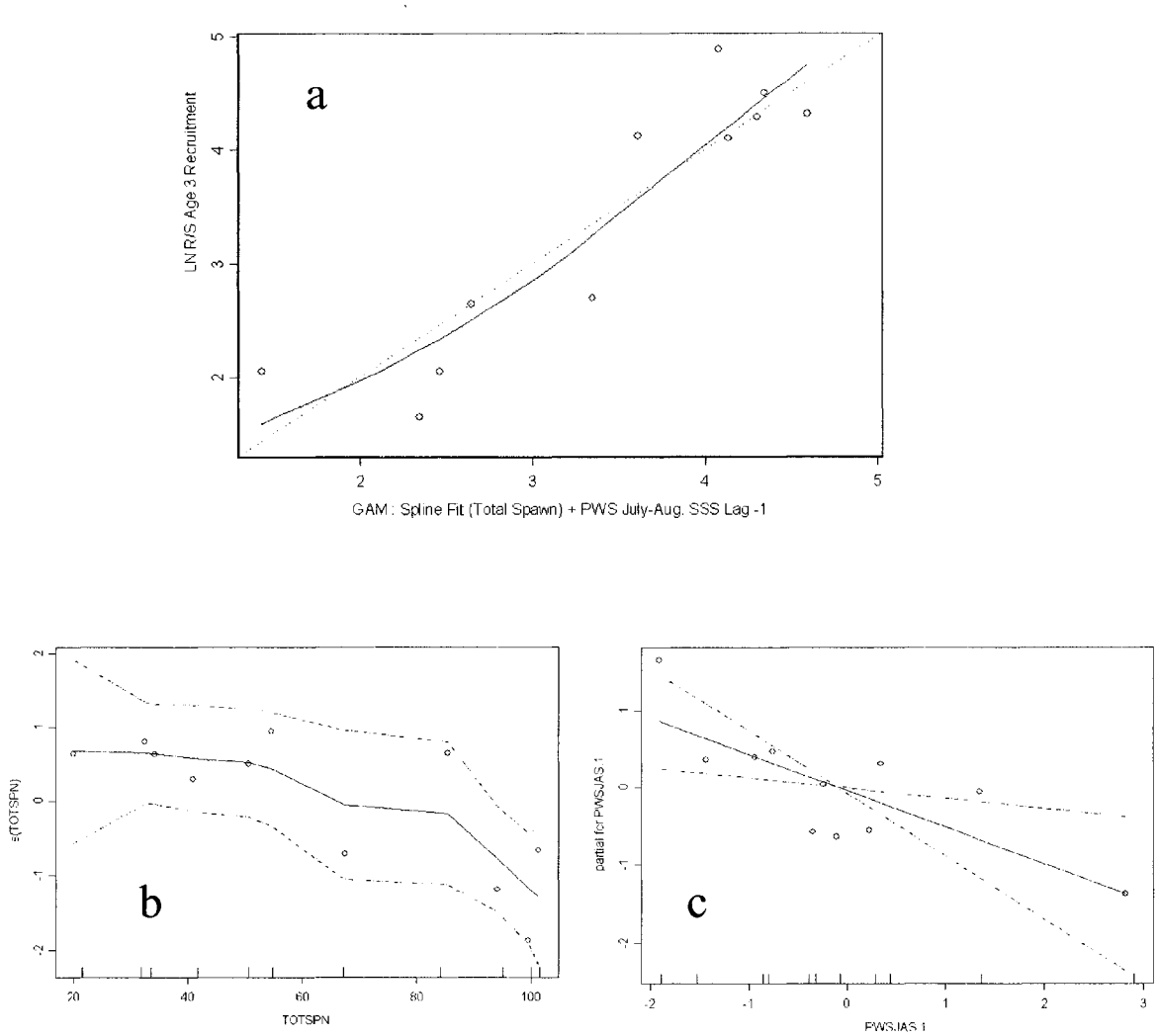


Figure 3.6. The two-parameter general additive modeling (gam); **(a)** recruitment model for log transformed recruit per spawner (R/S) age-3 ratio and the results of the smoothing function used to fit PWS total spawn (non-linear fit; **b**) and PWS SSS in July and August, -1 yr lag **(c)**.

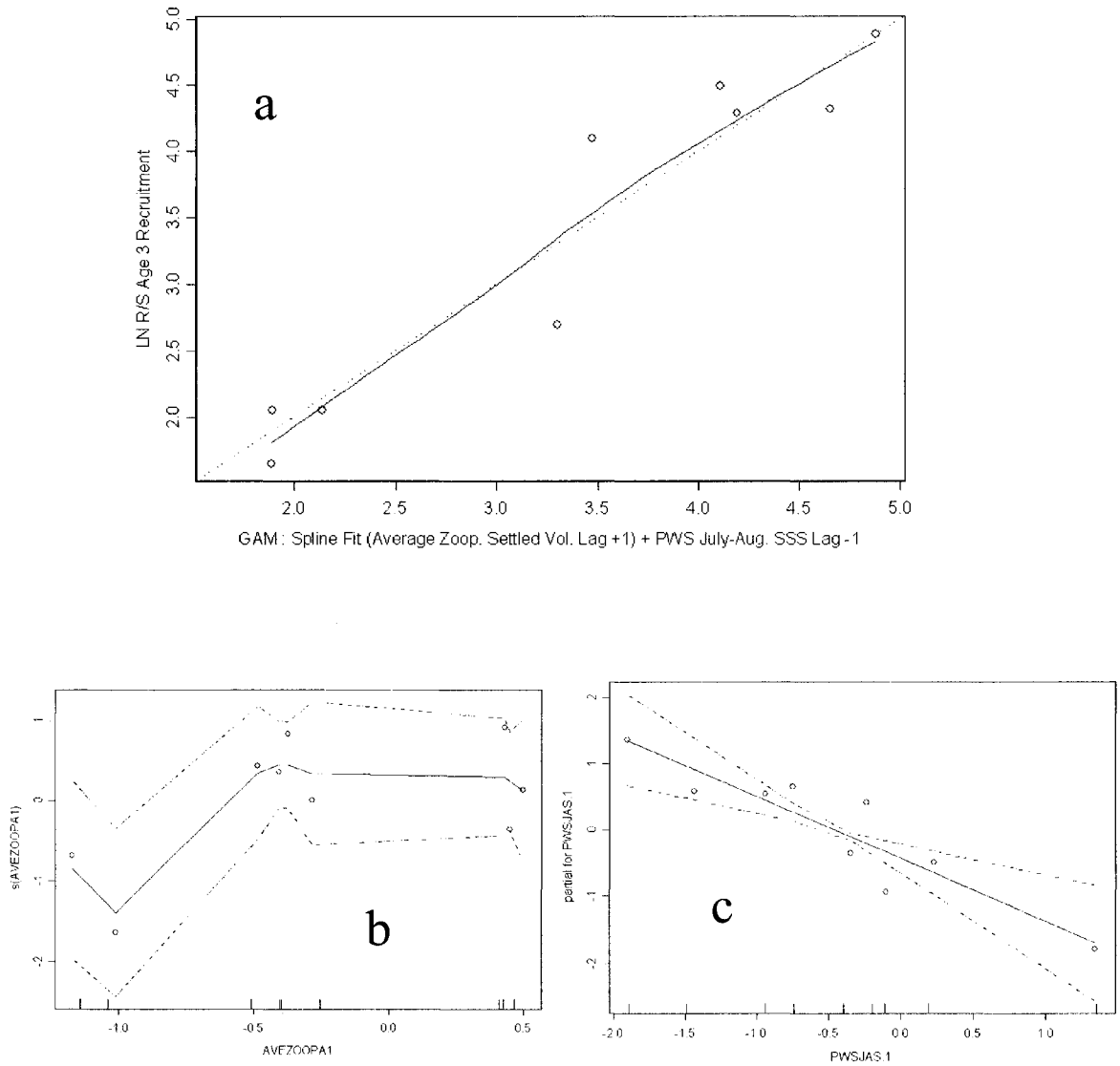


Figure 3.7. The two-parameter general additive modeling (gam); **(a)** recruitment model for log transformed recruit per spawner (R/S) age-3 ratio and the results of the smoothing function used to fit average zooplankton, +1 lag (non-linear; **b**) and PWS July-August salnity, -1 lag **(c)**.

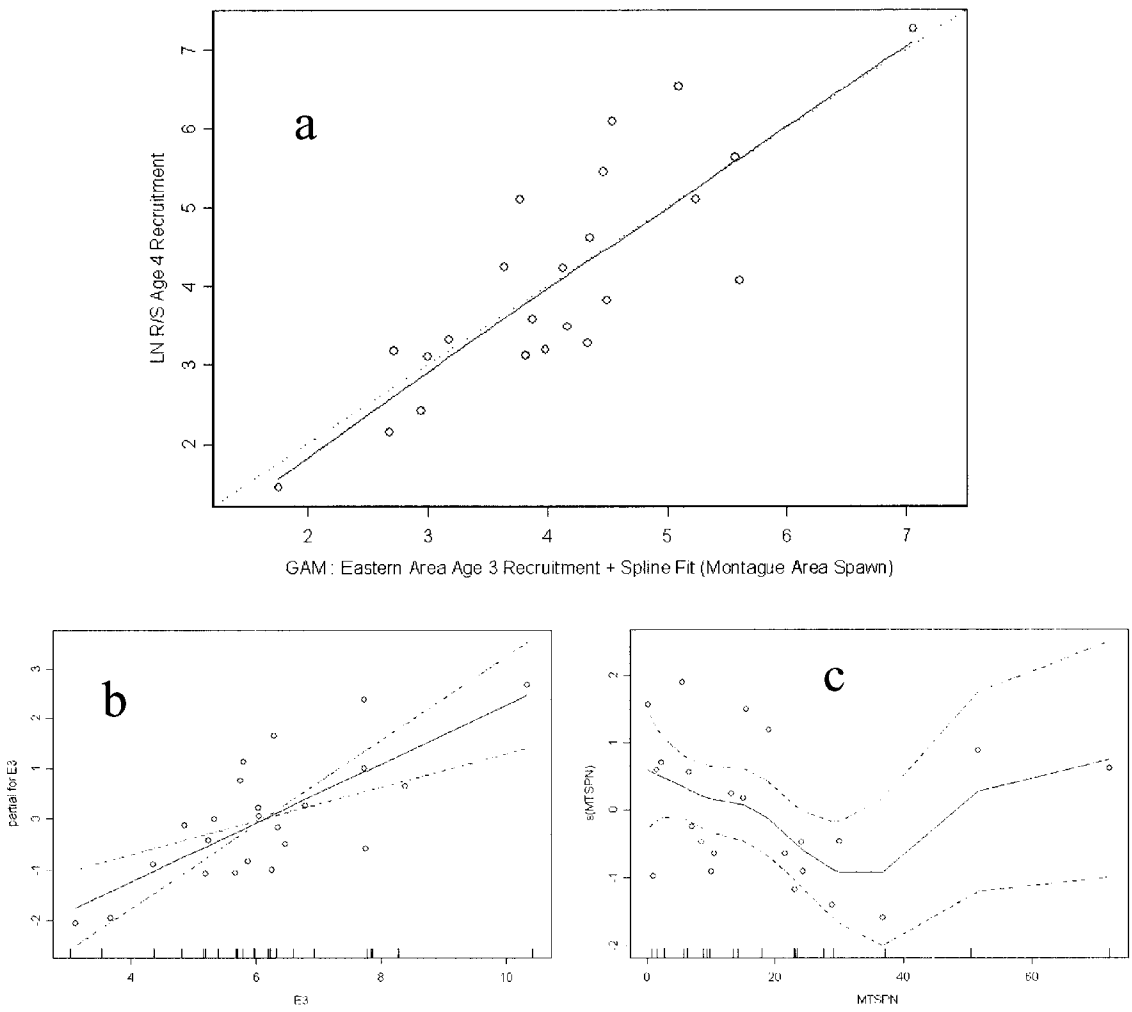


Figure 3.8. The two-parameter general additive modeling (gam); **(a)** recruitment model for log transformed recruit per spawner (R/S) age-4 ratio and the results of the smoothing function used to fit Eastern age-3 recruitment **(b)** and Montague spawn (non-linear; **c**).

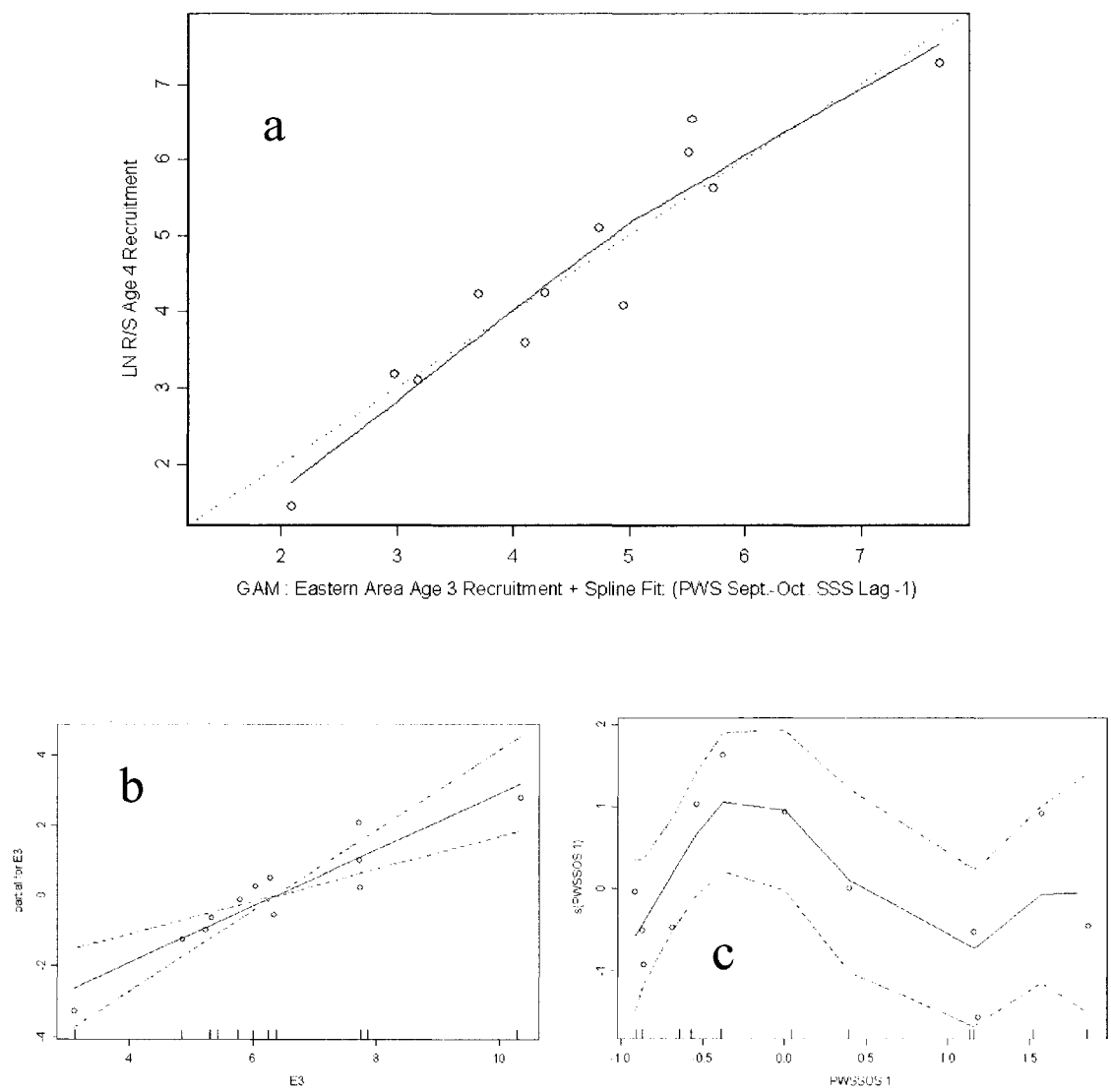


Figure 3.9. The two-parameter general additive modeling (gam); **(a)** recruitment model for log transformed recruit per spawner (R/S) age-4 ratio and the results of the smoothing function used to fit Eastern area age 3 recruitment **(b)** and PWS September-October SSS, -1 lag (non-linear; **c**).

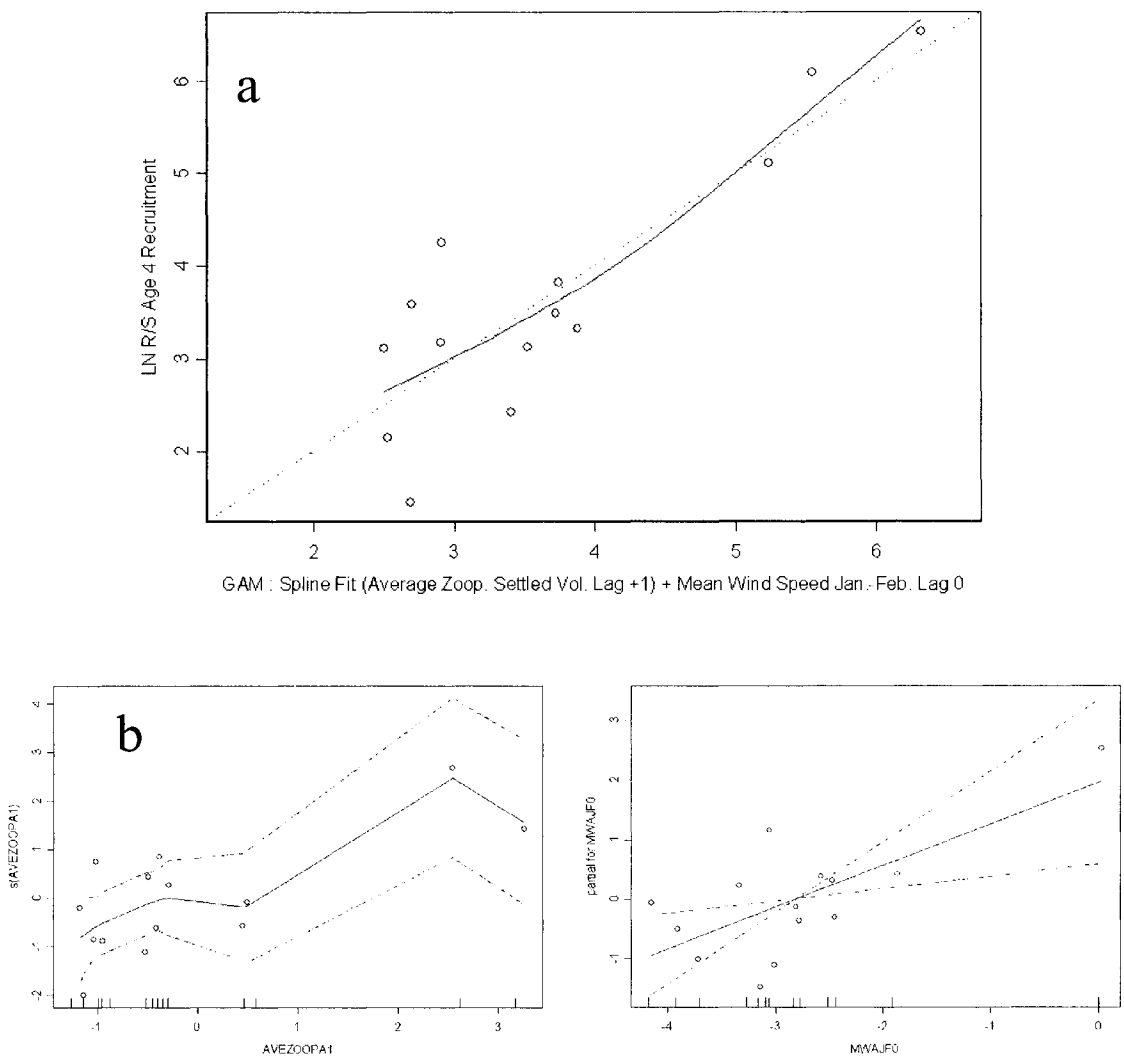


Figure 3.10. The two-parameter general additive modeling (gam); **(a)** recruitment model for log transformed recruit per spawner (R/S) age-4 ratio and the results of the smoothing function used to fit zooplankton, +1 lag (non-linear; **b**) and the mean wind speed anomaly for January-February, 0 lag **(c)**.

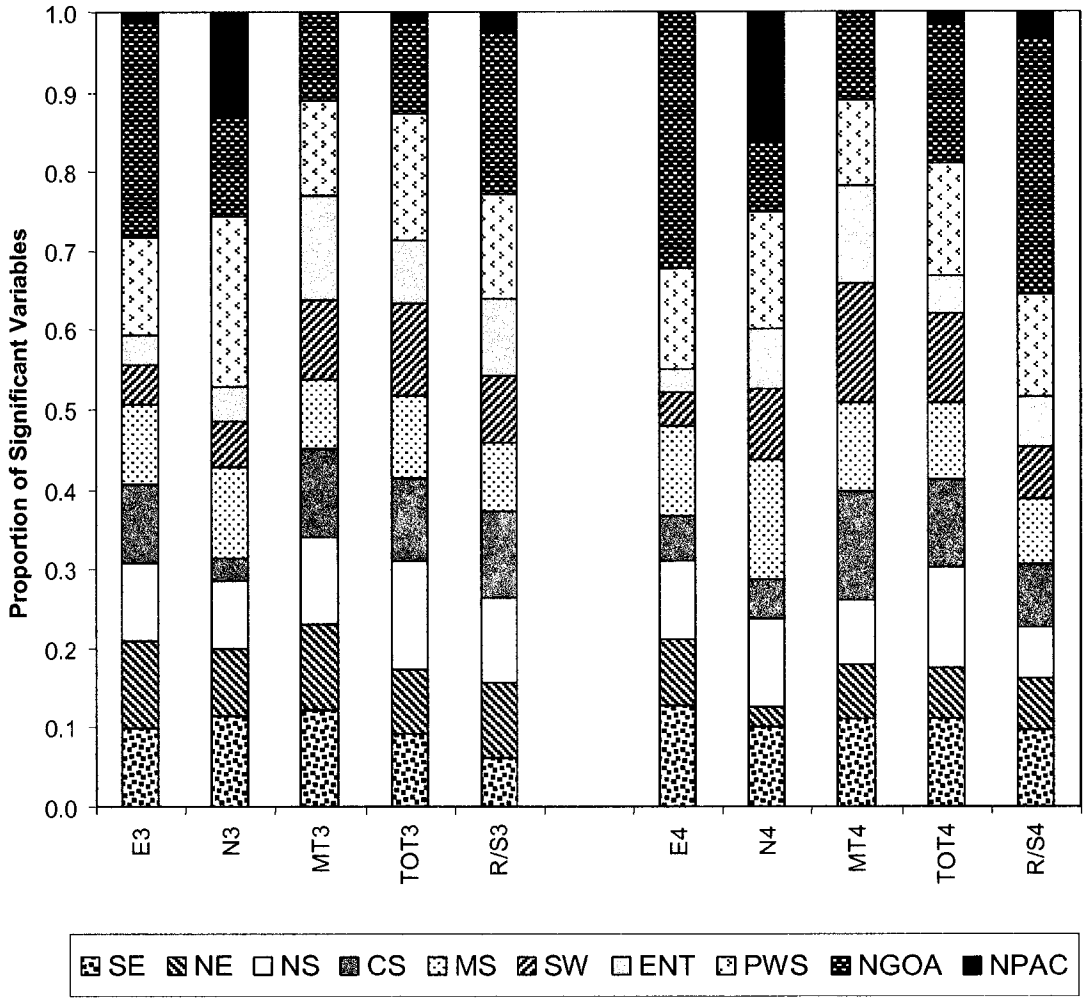


Figure 3.11. Allocation of significant environmental variables for each recruitment variable to local oceanographic regions (Southeast (SE), Northeast (NE), North Shore (NS), Central Sound (CS), Montague Strait (MS), Southwestern (SW), and the entrance (ENT) to PWS), for PWS as a whole, for N GOA regional forcing, and for the entire North Pacific (NPAC) for each recruitment response variable (Eastern age-3 and –4 recruitment (E3 & 4), Northern (N3 & 4), Montague (MT3 & 4), PWS total (TOT3 & 4), and PWS recruit-per-spawner ratios (LNR/S3 & 4).

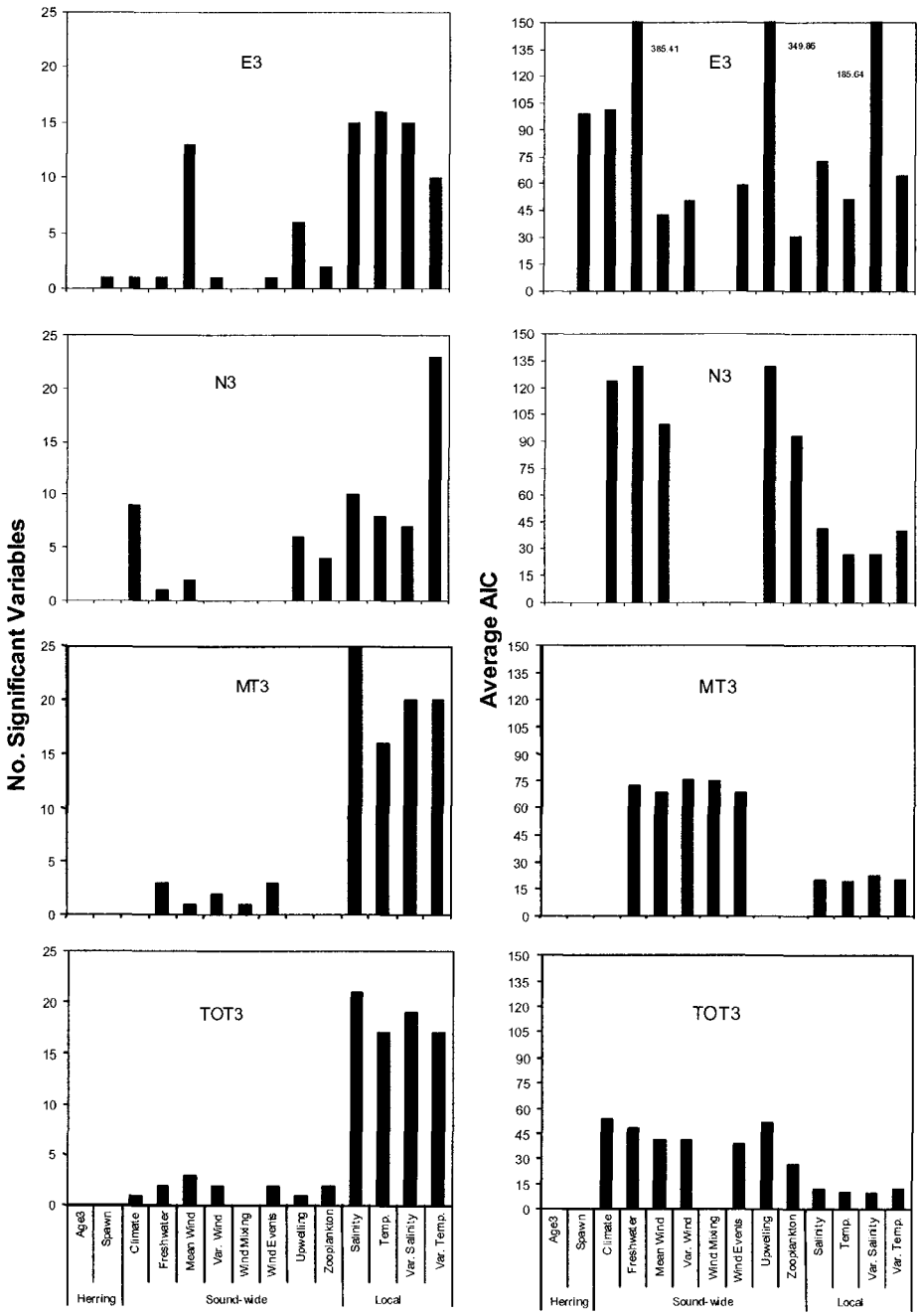


Figure 3.12. The distribution pattern of environmental variables significantly correlated to recruitment and the average model Akaike Information Criteria is categorized by variable type for each age-3 recruitment variable (Eastern (E3), Northern (N3), Montague (MT3), PWS total (TOT3).

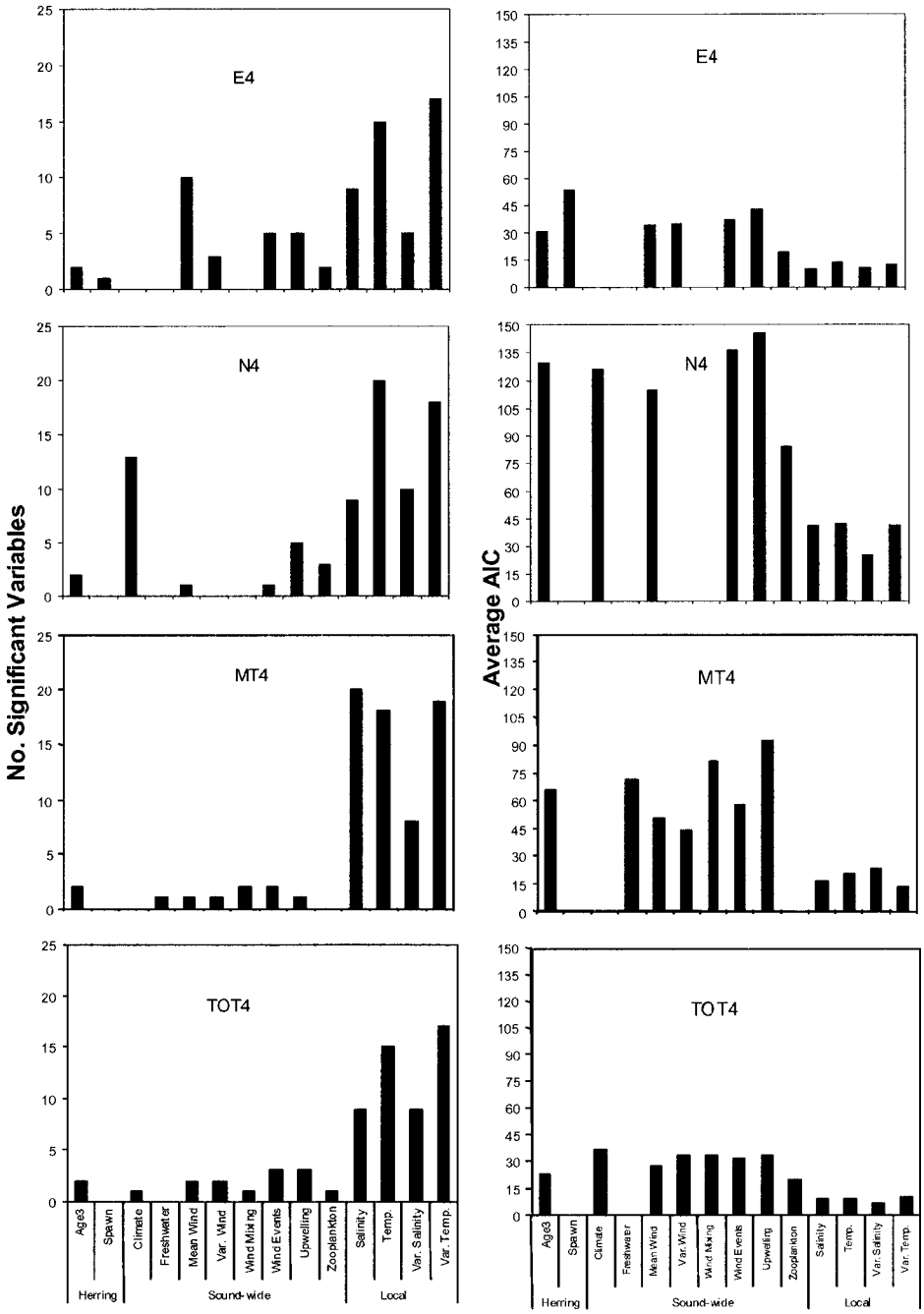


Figure 3.13. The distribution pattern of environmental variables significantly correlated to recruitment and the average model Akaike Information Criteria is categorized by variable type for each age-4 recruitment variable (Eastern (E4), Northern (N4), Montague (MT4), PWS total (TOT4).

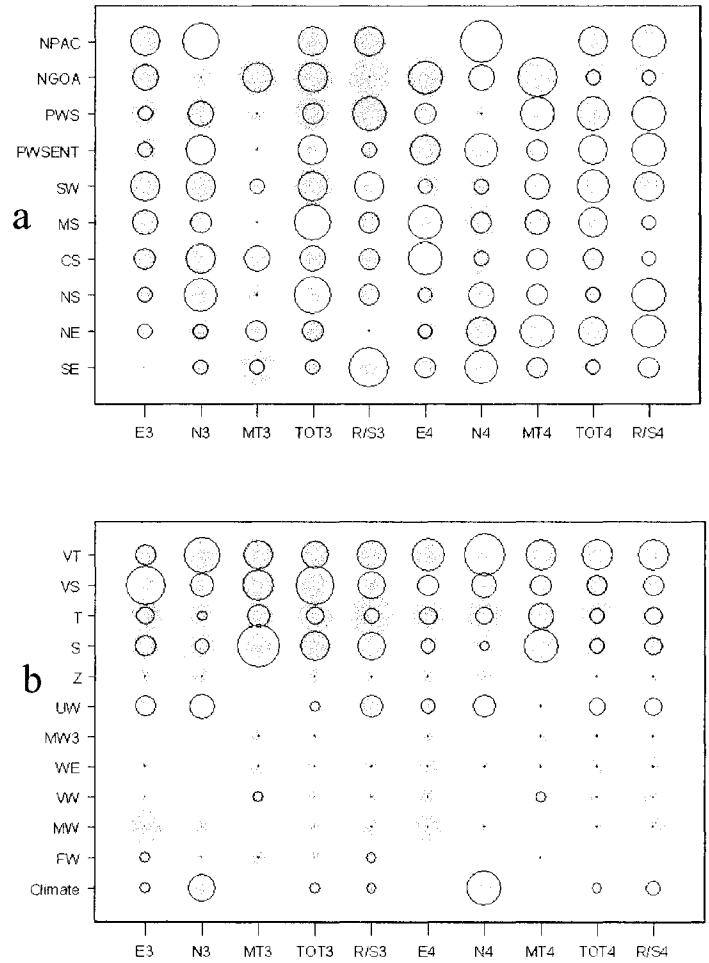
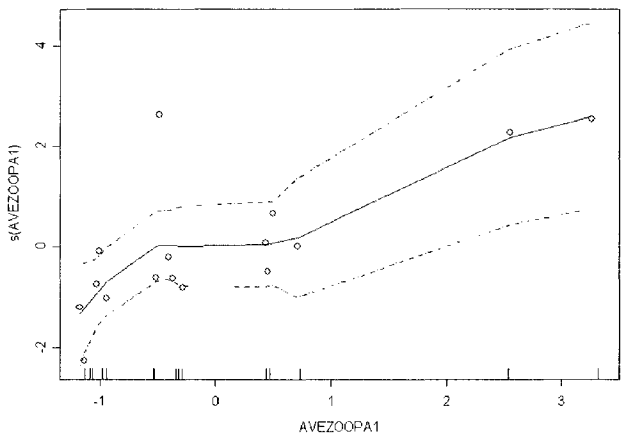
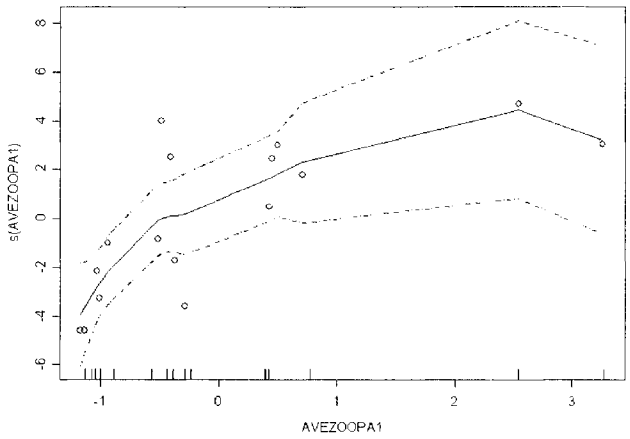


Figure 3.14 Variation among recruitment regions, Eastern age-3 and –4 recruitment (E3 & 4), Northern (N3 & 4), Montague (MT3 & 4), PWS total (TOT3 & 4), and PWS recruit-per-spawner ratios (LNR/S3 & 4)) in the number of positive (solid gray circles) and negative (open circles) correlations with environmental variables categorized by **a)** local oceanographic region (PWS oceanographic regions: (Southeast (SE), Northeast (NE), North Shore (NS), Central Sound (CS), Montague Strait (MS), Southwestern (SW), and the entrance (ENT) to PWS); PWS as a whole, N GOA, and the North Pacific (NPAC)) and by **b)** type of variable (climate-CLIM, freshwater discharge-FW, mean wind speed-MW, wind mixing-MW3, salinity-S, temperature-T, upwelling-UW, variance in salinity-VS, temperature-VT, and wind speed-VW, wind events-WE, and zooplankton-Z.

a. E4



b. N4



c. MT4

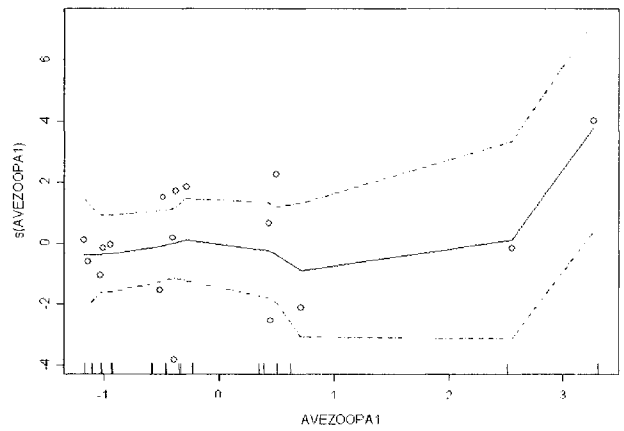
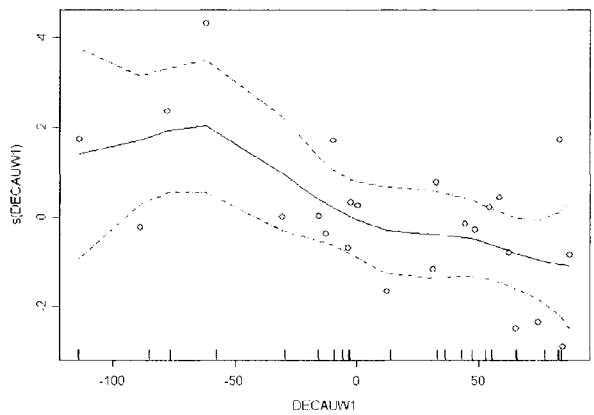
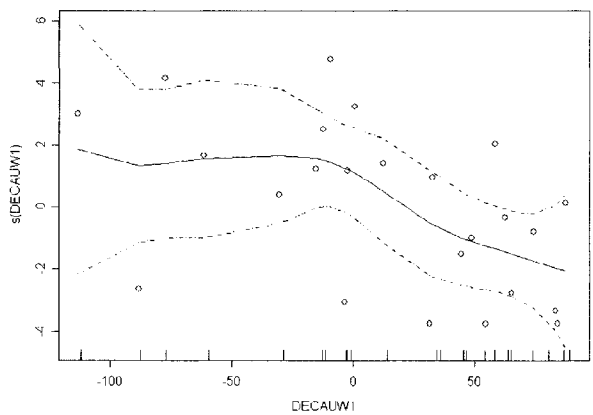


Figure 3.15. The results of the generalized additive model (gam) smoothing function for average zooplankton density lagged +1 and **a)** Eastern age-4 , **b)** Northern age-4, and **c)** Montague age-4 recruitment.

a. E3



b. N3



c. MT3

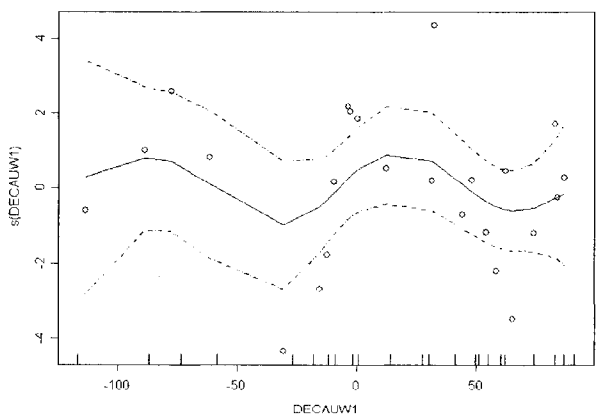


Figure 3.16. The results of the generalized additive model (gam) smoothing function for December upwelling lagged a year prior to the cohort year and **a)** Eastern age-3 , **b)** Northern age-3, and **c)** Montague age-3 recruitment.

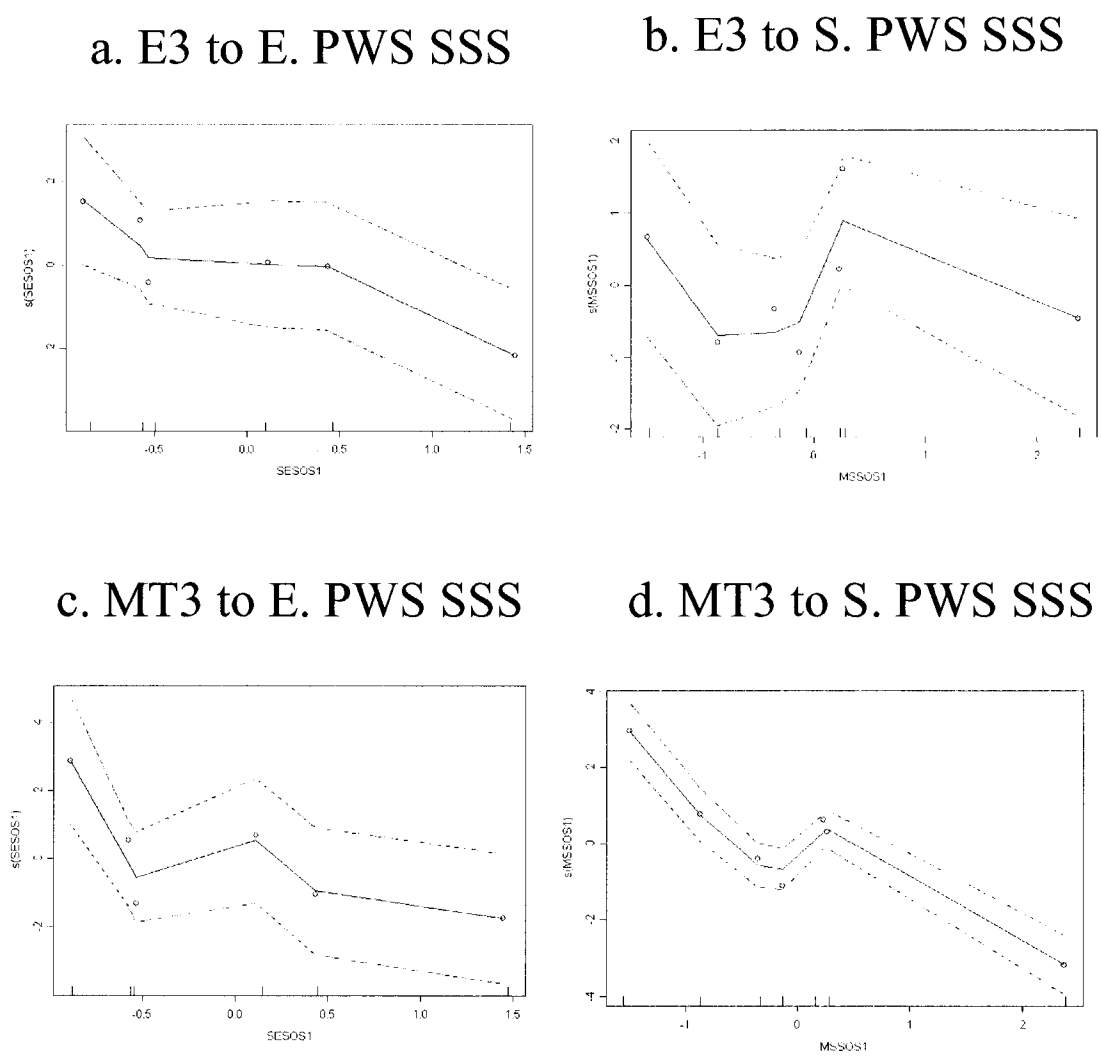


Figure 3.17. The results of the generalized additive model (gam) smoothing function for Eastern age-3 recruitment and PWS composite salinity in September and October, lagged +1 in eastern **(a)** versus southern PWS **(b)** as well as for Montague age-3 recruitment and PWS fall salinity in eastern **(c)** versus southern PWS **(d)**.

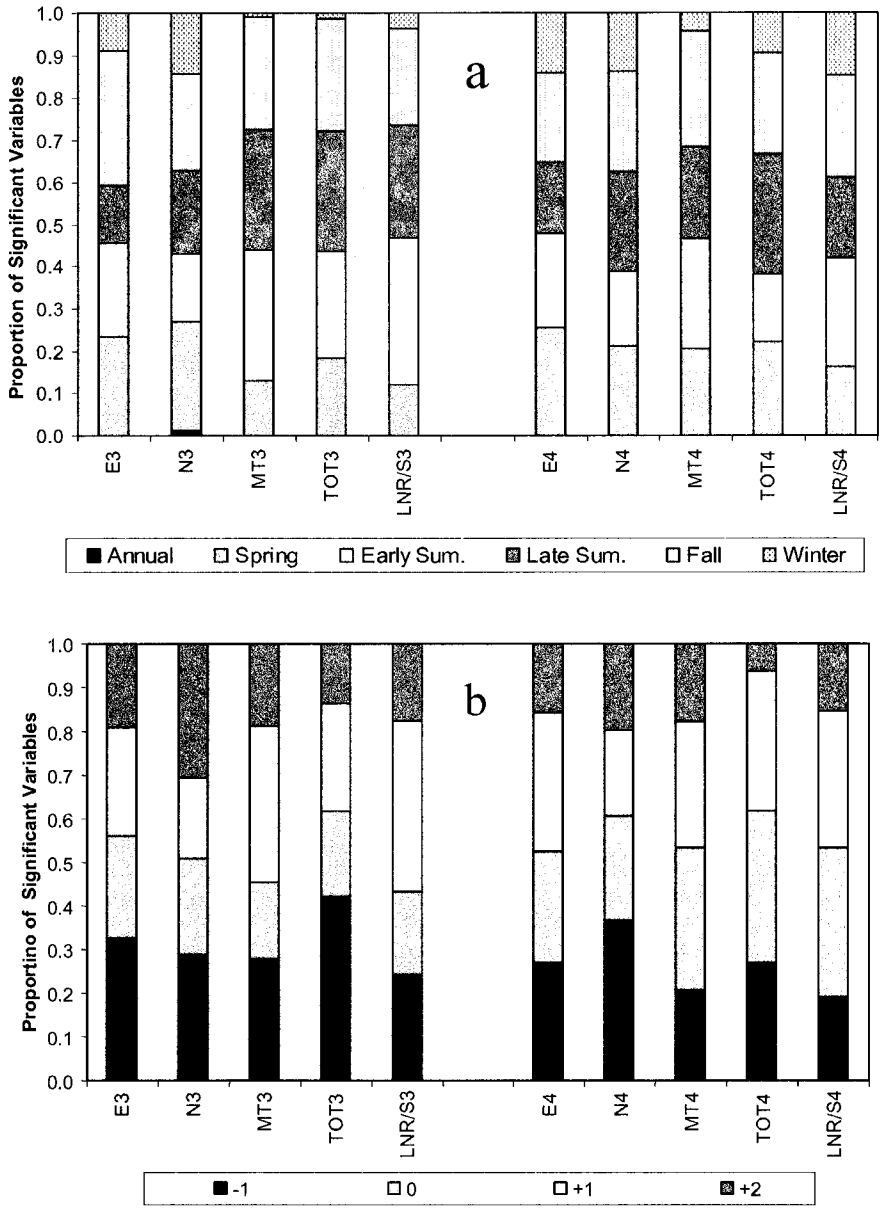
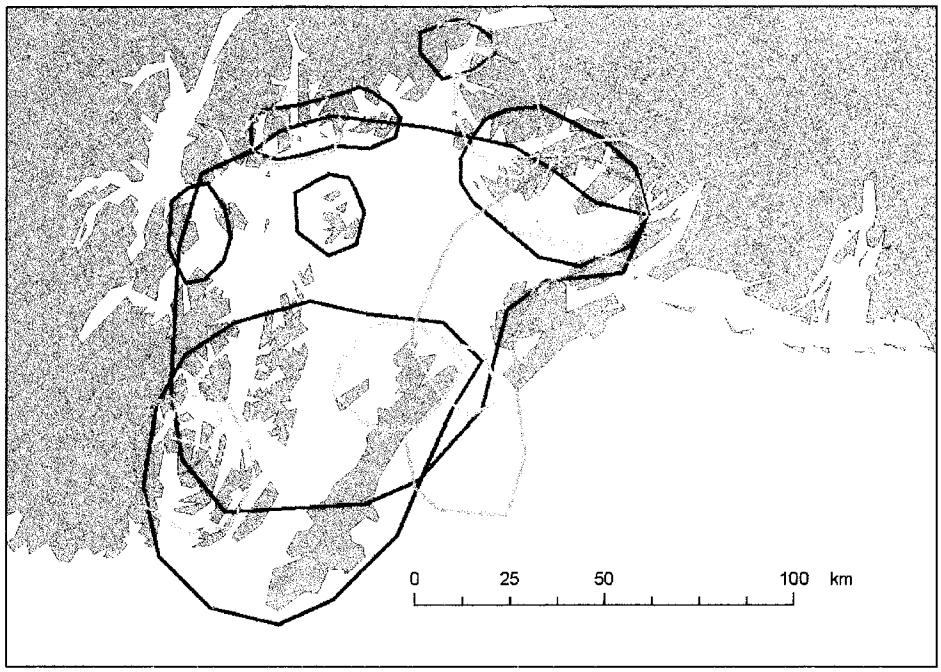


Figure 3.18. The proportion of environmental variables significantly related to recruitment by season **(a)** and by the year of the lag applied **(b)** for Eastern age-3 and –4 recruitment (E3 & 4), Northern (N3 & 4), Montague (MT3 & 4), PWS total (TOT3 & 4), and PWS recruit-per-spawner ratios (LNR/S3 & 4). Lag –1 is the year prior to the cohort year, 0 is the cohort year, lag +1 is the year proceeding and lag +2 is two years after the cohort year. Spring encompasses March-April; early summer, May-June; late summer, July-August; fall, September-November; and winter, December-February.



Period	Affected Life Stage	Outline Color	Critical Variables
1.Spring (March-April), Cohort Year +1	Age-0 juvenile at 1st birthday		**SALINITY (SE)**, SST, variance salinity, zooplankton density (upper 30 m in nursery bays), mean wind speed, wind mixing, upwelling
2. Late Summer (July-Aug.) Cohort Year –1	Adults-feeding	Blue	**SST, VARIANCE SST, VARIANCE SALINITY (NE)** salinity (upper 50 m)
3. Late Summer, Cohort Year	End of Larval Drift & Metamorphosis	Red	**SST (NE)**, salinity variance SST, variance salinity, (upper 20 m especially at mouths of nursery bays), wind mixing, variance mean wind speed, frequency of wind events over 25 knots
4. Late Summer, Cohort Year +1	Age-1 juveniles prior to 2nd overwintering period	Pink	**SST (NE) and SALINITY (SE)**, variance SST, variance salinity (upper 30 m < 1 km from shore in nursery bays)
5. Late Summer, Cohort Year +2	Age-2 juveniles leaving nursery areas and joining adult schools	Pink	**VARIANCE SST (SE)** , variance salinity (upper 30 m at mouths and exits of nursery bays)
6. Fall (Sept.-Nov.), Cohort Year –1	Adults-beginning overwintering		**VARIANCE SST (NE & SE), VARIANCE SALINITY (NE)**, salinity (upper 50 m), freshwater input, mean wind speed, variance in mean wind speed, frequency of wind events over 35 knots
7. Fall, Cohort Year	Age-0 juvenile-beginning 1st overwintering period	Pink	**SALINITY (NE)**, SST, variance salinity, variance SST (upper 30 m in nursery bays), mean wind speed, upwelling
8. Fall, Cohort Year +2	Age-2 immature herring 1st overwintering period with adult schools		**SALINITY (NE)**, SST, variance salinity, variance SST

Figure 3.19. Map and table showing the areas, life stage affected, and types of variables to monitor for each of the eight critical periods identified. The best fit variables and local region (Northeast, NE and Southeast, SE) are in capitals and bolded. Processes occurring in the outlined regions and time periods probably determine recruitment success to the three local populations and PWS as a whole.

Appendix I. The spawn and environmental variables with significant correlations to age 3 and 4 regional recruitment variables, PWS total recruitment, and PWS recruit-per-spawner ratios (R/S) including the correlation coefficient (r), the p-value, and the model Akaike Information Criteria (AIC) from the generalized additive model runs (low value is good fit). The total number of significant variables, the mean absolute value of r, the mean p-value, and the mean AIC value are summarized by lag and recruitment variable. The codes for the variables are listed in Table 1.

		Eastern Age 3				Northern Age 3				Montague Age 3				PWS Total Age 3				PWS R/S Age 3			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	CSJAS-1									9	-0.758	0.018	10.47					9	-0.664	0.051	7.89
	CSJAT-1													9	0.672	0.048	5.32	9	0.693	0.039	7.35
	CSJAVT-1													9	-0.600	0.088	6.21	9	-0.585	0.098	9.29
	CSMAS-1									12	0.594	0.054	20.67								
	CSMJVS-1	11	-0.635	0.066	379.13					11	-0.826	0.006	10.58	11	-0.841	0.004	6.48				
	CSSOS-1	11	0.650	0.042	24.35									11	0.698	0.025	17.04				
	CSSOT-1					11	0.635	0.048	51.006												
	CSSOVS-1	11	-0.631	0.051	86.65									11	-0.688	0.028	14.29				
	ENSOSP-1																	28	0.399	0.059	40.42
	ENTJAS-1									7	-0.933	0.007	6.45	7	-0.782	0.066	3.91				
	ENTJAT-1					7	0.764	0.077	9.92475	7	0.762	0.078	20.77	7	0.881	0.020	2.24	7	0.923	0.009	2.01
	ENTJAVT-1																	7	-0.759	0.080	4.04
	ENTMAS-1					7	-0.764	0.077	31.2305												
	ENTSOS-1	8	0.937	0.002	13.19									8	0.892	0.007	6.99				
	ENTSOVS-1																	8	-0.881	0.021	4.03
	FEBAUW-1					27	-0.328	0.118	155.923												
	HSEAJF-1									25	0.497	0.022	68.93								
	JANAUW-1					27	-0.560	0.004	119.88												
	MSJAS-1	9	-0.806	0.016	60.87									9	-0.859	0.006	2.77	9	-0.818	0.013	5.21
	MSJAVT-1					9	-0.859	0.006	39.2543												
	MSMAS-1	13	0.719	0.019	8.83					13	0.719	0.026	15.97	7	-0.355	0.004	20.10				
	MSMAT-1	13	0.660	0.038	10.33																
	MSMAVS-1	13	-0.646	0.044	375.84					13	-0.828	0.003	9.67	13	-0.807	0.005	8.48				
	MSMJVS-1	14	-0.561	0.092	200.82					14	-0.749	0.013	19.65	14	-0.706	0.022	17.68				
	MWASN-1	26	0.400	0.066	39.84																
	NEJAVS-1					3	-1.000	0.012	0.0081					3	-1.000	0.005	0.00	3	-1.000	0.016	0.01
	NEJAVT-1					3	-0.995	0.061	0.2193					3	-0.996	0.055	0.04	3	-0.995	0.065	0.10
	NEMAS-1									6	0.925	0.008	3.34	6	0.882	0.020	4.38				
	NEMAVS-1									6	-0.906	0.013	4.14	6	-0.849	0.032	5.52				
	NEMJS-1	5	-0.942	0.058	103.13																
Lag -1	NEMJVS-1	5	0.985	0.015	16.15					5	0.910	0.090	6.37	5	0.930	0.070	3.58				
	NEMJVT-1	5	0.915	0.085	10.27					5	0.903	0.097	6.88								
	NESOVS-1	3	-0.998	0.043	398.98					3	-0.993	0.073	0.05	3	-0.994	0.070	0.09	3	-0.997	0.048	0.09
	NESOVT-1					3	1.000	0.013	0.0093												
	NSJAS-1									6	-0.780	0.038	9.85								
	NSJAT-1					6	0.864	0.026	15.2804												
	NSJAVT-1					6	-0.954	0.003	1.77675												
	NSMAS-1													11	0.566	0.088	17.77				
	NSMAVS-1	11	-0.569	0.086	362.28									11	-0.665	0.036	14.56				
	NSMAVT-1					11	0.567	0.087	65.884									11	0.624	0.072	8.94
	NSSOS-1	8	0.744	0.055	33.86									8	0.812	0.027	12.02				
	NSSOVS-1	8	-0.737	0.059	206.06					8	-0.699	0.081	19.49	8	-0.840	0.018	10.39	8	-0.925	0.008	3.13
	NSSOVT-1																	8	0.735	0.096	9.92
	PWSJAS-1									12	-0.633	0.001	16.19	12	-0.735	0.010	5.61	12	-0.603	0.049	10.74
	PWSJAT-1									12	0.566	0.070	36.01								
	PWSMAVS-1	15	-0.591	0.043	321.89					15	-0.527	0.078	41.46	15	-0.723	0.008	12.41				
	PWSMJS-1					19	0.517	0.049	82.537					19	0.476	0.073	28.16				
	PWSMJVS-1	19	-0.460	0.084	141.98					19	-0.460	0.084	66.96	19	-0.618	0.014	22.50				
	PWSMJVT-1					19	-0.569	0.027	76.1163												
	PWSSOS-1	15	0.749	0.003	22.86									15	0.644	0.000	11.37	15	0.668	0.018	17.88
	PWSSOT-1					15	0.600	0.030	83.0002												
	PWSSOVS-1	15	-0.481	0.096	100.16									15	-0.543	0.055	27.89	15	-0.519	0.083	23.55
	SEJAT-1									4	0.916	0.084	0.75								
	SEJAVT-1					4	0.950	0.050	0.9776												
	SEMAVS-1	8	-0.720	0.068	21.18					8	-0.914	0.004	5.26	8	-0.873	0.010	4.86				
	SEMAVT-1	8	-0.751	0.052	19.83					8	-0.899	0.006	6.13	8	-0.921	0.003	3.12				
	SEMJVS-1					9	-0.684	0.090	27.6472												
	SEPAFWD-1									27	0.520	0.009	74.22	27	0.450	0.027	48.60				
	SWJAT-1													9	0.717	0.045	4.75	9	0.712	0.047	6.86
	SWMJS-1									14	0.643	0.045	45.19	14	0.601	0.066	20.17				
	SWSOS-1	12	0.610	0.061	34.80									12	0.730	0.017	18.81				
Lag -1	Summary	# Var.	Avg |r|	Avg	Avg	# Var.	Avg |r|	Avg	Avg	# Var.	Avg |r|	Avg	Avg	# Var.	Avg |r|	Avg	Avg	# Var.	Avg |r|	Avg	Avg
		24	0.704	0.052	124.72	17	0.742	0.046	44.746	25	0.762	0.040	21.02	34	0.751	0.032	11.41	18	0.750	0.048	8.97

Appendix I continued.

		Eastern Age 3				Northern Age 3				Montague Age 3				PWS Total Age 3				PWS R/S Age 3			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	AVEZOOPA0					19	0.410	0.115	104.243												
	CSJAT0	9	0.648	0.059	15.34																
	CSMJVT0					11	-0.661	0.038	38.142												
	CSSOVT0																	11	-0.682	0.030	16.69
	ENTJAS0									7	-0.928	0.008	2.51								
	ENTJAT0																	7	0.840	0.036	1.42
	ENTJAVT0																	7	-0.837	0.038	2.05
	ENTMAVT0	7	0.877	0.010	34.86									7	0.861	0.013	9.58	7	0.941	0.005	3.36
	ENTMJVS0									9	0.624	0.098	15.09								
	ENTSOS0									8	-0.629	0.095	28.42								
	HSEAA0									26	0.560	0.007	63.46	26	0.653	0.001	34.38	26	0.578	0.006	35.05
	HSEAMA0									26	0.495	0.019	73.98								
	MARAFWD0									26	0.574	0.003	68.19								
	MSJAT0	9	0.732	0.039	23.73	9	0.796	0.018	32.1315					9	0.830	0.011	3.63	9	0.725	0.042	6.41
	MSJAVT0	9	-0.775	0.024	119.15	9	-0.743	0.035	15.2701					9	-0.800	0.017	4.19	9	-0.801	0.017	4.84
	MSMAS0									13	-0.558	0.074	25.48								
	MSSOT0	7	-0.706	0.076	57.65									7	-0.755	0.050	6.04				
	MW3AA0									26	0.506	0.016	68.79	26	0.502	0.017	44.85				
	MW3AMA0									26	0.489	0.021	74.53								
	MWAD0	27	0.579	0.004	44.07																
	MWAJF0	26	0.560	0.008	46.10																
	MWAMA0	26	0.477	0.025	52.44																
	MWASN0	26	0.523	0.013	48.14																
	NEJAT0	3	0.998	0.041	158.18					3	-0.997	0.048	0.01	3	0.996	0.055	0.04				
	NEMAS0									6	-0.743	0.091	2.74								
	NEMAVT0																	6	-0.798	0.057	11.03
Lag 0	NEMJS0	5	-0.858	0.063	168.15																
	NEMJT0	5	0.825	0.086	75.18																
	NEMJVS0	5	0.835	0.079	7.84																
	NESOS0									3	1.000	0.019	0.00								
	NESOVS0																	3	-1.000	0.010	0.01
	NSJAS0													6	-0.843	0.035	1.28				
	NSJAT0	6	0.832	0.040	63.17	6	0.808	0.052	4.96155					6	0.873	0.023	1.06				
	NSJAVT0													6	-0.741	0.092	2.00				
	NSMJT0																	12	0.841	0.004	8.05
	NSMJVT0									12	-0.616	0.058	19.88								
	NSSOT0													8	-0.636	0.090	19.01				
	PKZOOPA0					19	0.574	0.020	84.0514												
	PWSJAS0									*12*	*-0.612*	*0.045*	*15.39*								
	PWSJAT0	12	0.583	0.060	22.69									12	0.738	0.010	6.10				
	PWSMJT0													19	0.539	0.031	34.47	19	0.569	0.030	25.78
	PWSMJVT0					19	-0.499	0.049	93.1511												
	PWSSOVS0									15	0.487	0.078	41.77								
	SEJAVS0					4	0.942	0.058	2.3168												
	SEJAVT0					4	0.976	0.024	1.2998												
	SEMJS0													9	-0.672	0.068	20.35				
	SEMJVT0					9	-0.791	0.019	25.7549												
	SEPAUW0	26	-0.526	0.008	393.27	26	-0.521	0.009	127.333									26	-0.411	0.052	44.14
	SESOVS0					6	0.808	0.052	5.37405												
	SWJAT0													9	0.802	0.017	3.00	9	0.738	0.037	5.35
	SWMJVT0					14	-0.521	0.100	75.0729												
	VMWAA0	26	0.528	0.011	50.45									26	0.602	0.003	38.26	26	0.603	0.004	33.51
	VMWAMA0									26	0.458	0.032	77.36								
Lag 0 Summary		**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		17	0.697	0.038	81.20	13	0.696	0.045	46.854	16	0.642	0.045	36.10	16	0.740	0.033	14.27	14	0.740	0.026	14.12

Appendix I continued.

	Eastern Age 3				Northern Age 3				Montague Age 3				PWS Total Age 3				PWS R/S Age 3			
	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
AVEZOOPA1	19	0.603	0.010	25.17	19	0.520	0.032	99.27					19	0.677	0.003	24.99	19	0.675	0.004	19.36
CSJAVT1									9	0.724	0.027	12.84								
CSMAT1	12	0.510	0.090	29.30													12	0.546	0.066	23.60
CSMAVT1	12	0.854	0.000	19.32									12	0.667	0.018	17.37	12	0.722	0.008	16.08
CSSOS1									11	-0.618	0.043	42.42					11	-0.523	0.099	14.53
CSSOT1									11	0.644	0.033	40.21					11	0.615	0.044	12.44
CSSOVS1									11	0.703	0.016	34.67	11	0.576	0.064	17.50				
DECAUW1	25	-0.666	0.004	388.32	25	-0.501	0.013	130.80									25	-0.571	0.004	36.80
ENSOSP1																	25	-0.469	0.018	44.64
ENTJAVT1									7	0.787	0.063	12.01	7	0.846	0.034	3.97				
ENTMAS1									7	-0.694	0.084	30.49								
ENTMAT1	7	0.780	0.039	10.51																
ENTMAVT1									7	-0.867	0.012	14.61								
ENTSOT1									8	0.643	0.086	43.43								
ENTSOVS1									8	0.663	0.073	41.42	8	0.764	0.027	6.80				
ENTSOVT1					8	0.630	0.094	22.13												
GFEAJF1	25	0.627	0.002	59.08																
MSJAT1									9	-0.778	0.023	15.43								
MSMAVT1					13	-0.598	0.052	43.89												
MSMJS1									14	-0.604	0.038	52.77	14	-0.611	0.035	20.56	14	-0.575	0.064	13.42
MSMJVT1									14	0.614	0.034	51.70	14	0.551	0.063	22.83	14	0.748	0.008	8.85
MSSOS1									7	-0.881	0.009	6.71								
MSSOT1																	7	0.698	0.081	5.42
MSSOVT1					7	0.715	0.071	22.95												
MWAJF1	25	0.601	0.003	38.15																
MWAMA1	25	0.626	0.002	36.28																
NEJAT1																	3	-0.997	0.051	0.04
NEMAT1	6	0.817	0.047	19.07													6	0.904	0.014	4.22
NEMAVT1									6	0.854	0.030	16.23								
NESOVT1																	3	0.995	0.064	0.15
NOVAFWD1																	25	-0.493	0.017	40.17
NSJAT1									6	-0.889	0.018	4.90					6	-0.770	0.073	1.33
NSJAVT1									6	0.905	0.013	4.21								
NSMAT1	11	0.620	0.042	16.28									11	0.738	0.009	11.94	11	0.782	0.004	9.27
NSSOVT1									7	-0.851	0.015	21.35	7	-0.729	0.063	7.29	7	-0.925	0.003	1.08
PKZOOPA1	19	0.688	0.003	36.13	19	0.608	0.010	85.75					19	0.610	0.009	29.97	19	0.662	0.005	19.99
PWSJAT1									12	-0.536	0.089	30.67								
PWSJAVS1									12	0.569	0.057	28.12								
PWSJAVT1									12	0.719	0.013	20.77								
PWSMAT1	15	0.549	0.052	27.41									15	0.597	0.031	20.61	15	0.641	0.018	20.10
PWSMAVT1	15	0.656	0.015	35.08	15	0.505	0.078	57.36					15	0.492	0.088	24.31	15	0.552	0.051	23.72
PWSMJVT1					18	-0.440	0.088	64.66												
PWSSOS1									14	-0.570	0.033	58.07								
PWSSOT1																	14	0.560	0.046	14.84
PWSSOVS1									14	0.861	0.000	22.29	14	0.753	0.002	14.26	14	0.591	0.033	14.06
PWSSOVT1					14	0.514	0.060	51.65												
SEJAVS1									4	0.991	0.009	0.51	4	0.994	0.006	0.28	4	0.994	0.006	0.21
SEJAVT1									4	0.940	0.060	3.21	4	0.942	0.058	2.88	4	0.920	0.080	2.62
SEMAS1	8	0.949	0.000	2.39	8	0.718	0.045	20.54									8	0.616	0.104	11.74
SEMAT1									8	0.638	0.089	34.95								
SEPAFWD1	25	-0.432	0.035	385.41																
SESOS1	6	-0.881	0.020	93.67																
SESOVS1									6	0.818	0.047	7.37	6	0.834	0.039	6.31				
SWJAS1									11	0.441	0.013	48.35								
SWJAT1									9	-0.895	0.003	4.95								
SWMAT1	14	0.732	0.007	20.74									14	0.706	0.010	15.67	14	0.813	0.001	11.39
SWMAVT1									14	-0.574	0.051	41.27								
SWMJS1					14	0.511	0.089	42.69												
SWSOS1									12	-0.716	0.009	43.08	12	-0.663	0.019	16.43	12	-0.583	0.070	13.35
SWSOT1																	12	0.590	0.056	13.19
SWSOVS1	12	0.650	0.022	88.02					12	0.697	0.012	45.43	12	0.702	0.011	17.05	12	0.655	0.029	11.54
Lag +1 SWSOVT1									12	0.556	0.061	61.01	12	0.608	0.036	21.16				
Lag +1 Summary	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
	18	0.673	0.022	73.91	11	0.569	0.057	58.336	32	0.727	0.036	27.98	20	0.703	0.031	15.06	29	0.697	0.039	14.04

Appendix I. continued.

		Eastern Age 3				Northern Age 3				Montague Age 3				PWS Total Age 3				PWS R/S Age 3			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	ALPI2					24	0.404	0.050	146.12												
	APRAUW2	24	0.496	0.014	293.21																
	CSMAVT2									12	-0.710	0.010	25.50								
	CSMJT2	11	-0.598	0.052	133.95									11	-0.619	0.042	14.10				
	CSMJVT2	11	-0.645	0.032	220.29									11	-0.542	0.085	16.15				
	CSSOS2									11	-0.693	0.018	11.74								
	CSSOT2									11	0.746	0.008	10.04					11	0.562	0.072	23.43
	ENTMAT2													7	0.672	0.099	10.14	7	0.761	0.047	10.91
	ENTMJS2																	9	0.851	0.007	8.29
	ENTSOT2									8	0.860	0.004	5.49								
	ENTSOVT2									8	-0.679	0.064	13.09								
	JANAUW2	24	-0.475	0.019	388.12	24	-0.499	0.013	131.24					24	-0.388	0.061	51.78	24	-0.515	0.012	39.03
	JUNEAUW2	24	0.439	0.032	252.67													24	0.468	0.024	41.44
	MSMJS2					14	0.676	0.011	49.16												
	MSMJVT2					14	-0.604	0.029	57.48												
	MSSOS2					7	0.759	0.048	30.29												
	MSSOVS2																	7	-0.802	0.030	9.82
	MWAMJ2																	25	0.492	0.020	35.13
	NEMAS2					6	0.795	0.059	8.74												
	NEMJS2					5	-0.834	0.079	7.08	5	0.835	0.079	8.04								
	NEMJT2					5	0.893	0.041	4.72												
	NSJAVS2	6	-0.786	0.064	300.28									6	-0.867	0.025	4.93	6	-0.873	0.023	6.64
	NSMAVT2	10	0.611	0.060	25.42	10	0.608	0.062	48.13	10	0.578	0.080	35.43	10	0.758	0.011	10.56	10	0.626	0.053	19.16
	NSMJS2	9	0.639	0.064	17.14																
Lag +2	NSMJVS2					10	-0.645	0.042	28.67												
	NSSOS2									7	-0.769	0.043	8.87								
	NSSOT2									7	0.797	0.032	7.92								
	NSSOVS2									7	0.768	0.044	8.90								
	PDOW2					24	0.501	0.013	130.81												
	PWSMAVT2	15	0.656	0.034	35.08	14	0.690	0.009	45.36					14	0.555	0.049	28.32				
	PWSMJS2					17	0.469	0.067	81.74												
	PWSMJVS2					17	-0.426	0.100	85.77												
	PWSMJVT2					17	-0.488	0.055	79.80												
	PWSSOT2																	14	0.514	0.060	29.92
	SEJAVT2									4	-0.975	0.025	0.08								
	SEMAT2					8	-0.776	0.024	13.27												
	SEMAVS2									8	0.640	0.088	10.89	8	0.761	0.028	2.08				
	SEMAVT2									8	0.635	0.091	11.00								
	SEMJS2	9	0.589	0.095	23.79					9	0.752	0.019	10.66	9	0.703	0.035	4.69	9	0.597	0.090	10.90
	SEMJT2	9	-0.634	0.067	142.04																
	SEMJVS2	9	-0.684	0.042	42.39																
	SEMJVT2	9	-0.692	0.039	123.21																
	SESOT2																	6	0.845	0.034	1.96
	SWJAVS2	9	-0.643	0.062	220.52																
	SWMAVS2									14	0.476	0.100	50.00								
	SWMAVT2					14	0.708	0.007	43.18					14	0.560	0.047	28.09				
	SWSOS2					12	0.547	0.066	62.92												
	SWSOT2									12	0.536	0.072	21.26	12	0.499	0.099	20.42	12	0.522	0.082	26.07
	YMWAA2									26	-0.525	0.008	73.66								
Lag +2 Summary		**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		14	0.613	0.048	158.44	18	0.629	0.043	58.582	17	0.706	0.046	18.39	11	0.629	0.053	17.39	13	0.648	0.043	20.21
Age 3 Summary		**73**	**0.677**	**0.041**	**108.52**	**59**	**0.665**	**0.047**	**51.97**	**90**	**0.718**	**0.041**	**25.68**	**81**	**0.721**	**0.035**	**13.69**	**74**	**0.709**	**0.039**	**13.91**

Appendix I. continued.

		Eastern Age 4				Northern Age 4				Montague Age 4				PWS Total Age 4				PWS R/S Age 4			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	CSMAT-1									12	-0.589	0.073	12.57								
	CSSOVT-1					11	-0.708	0.031	43.6718												
	ENTJAVT-1					7	-0.778	0.068	31.471												
	ENTMJS-1					9	0.738	0.094	38.2387												
	FEBAUW-1					27	-0.436	0.038	149.719												
	GFEASN-1	26	0.436	0.048	32.96																
	HSEAJF-1					25	0.462	0.031	136.569												
	JANAUW-1					27	-0.445	0.034	139.988												
	MSJAS-1																	9	-0.626	0.097	5.40
	MSJAT-1					9	0.763	0.028	24.949												
	MSMAS-1	7	0.503	0.063	12.87					7	0.614	0.002	2.28	7	0.469	0.004	4.67	7	0.502	0.015	7.39
	MSMAT-1					13	0.623	0.073	51.3358												
	MSMAVS-1					13	-0.604	0.085	82.6933												
	MSMAVT-1	13	-0.690	0.040	11.11													13	-0.655	0.056	9.29
	MSMJS-1	14	0.704	0.034	13.49	14	0.767	0.034	46.4555	14	0.658	0.054	10.94	14	0.744	0.021	9.40				
	MSSOS-1	7	0.806	0.099	6.59	7	0.847	0.070	32.5554												
	MSSOVT-1									7	0.865	0.059	4.58								
	MWAJF-1					25	0.594	0.006	115.023												
	MWASN-1	26	0.490	0.024	30.91													26	0.430	0.052	31.39
	NEJAT-1	3	0.997	0.050	0.15									3	1.000	0.016	0.01				
	NEJAVS-1					3	-0.989	0.094	2.68014												
	NEMAS-1									6	0.928	0.023	1.32								
	NEMAT-1									6	-0.924	0.025	1.38								
	NEMAVT-1	6	-0.910	0.032	2.20									6	-0.974	0.005	0.15	6	-0.939	0.018	0.86
	NESOVT-1									3	-0.993	0.076	0.04								
Lag -1	NSJAT-1	6	0.876	0.022	3.29	6	0.882	0.020	11.0142					6	0.732	0.098	3.88				
	NSJAVS-1					6	-0.833	0.039	25.1843												
	NSJAVT-1	6	-0.776	0.070	5.64	6	-0.979	0.001	5.18055												
	NSMAVS-1													11	0.612	0.060	8.31				
	NSMAVT-1					11	0.589	0.095	72.8205	11	0.667	0.050	17.50	11	0.601	0.067	8.49				
	NSMJVS-1													12	-0.625	0.098	5.22				
	NSSOVS-1	8	-0.913	0.011	4.73									8	-0.680	0.021	3.03	8	-0.961	0.002	1.37
	NSSOVT-1	8	0.867	0.025	7.09									8	0.916	0.010	2.18	8	0.916	0.010	2.85
	PDOW-1					27	0.433	0.039	150.161												
	PMDOSP-1					25	-0.477	0.021	142.761												
	PMDOSU-1					25	-0.430	0.041	150.618												
	PMDOW-1					26	-0.511	0.013	136.368												
	PWSMAS-1									15	0.574	0.065	21.07								
	PWSMJS-1									19	0.530	0.051	46.98								
	PWSMJVT-1					19	-0.537	0.048	89.6575					19	-0.467	0.092	18.33				
	PWSSOS-1													15	0.549	0.064	23.07	15	0.535	0.073	25.82
	PWSSOT-1					15	0.637	0.026	81.4369												
	PWSSOVS-1	15	-0.540	0.070	31.65																
	SEMAT-1	8	-0.785	0.064	3.46					8	-0.867	0.025	1.73	6	-0.914	0.011	1.16	8	-0.624	0.185	5.01
	SESOVT-1	6	-0.925	0.024	0.26	6	-0.850	0.068	7.15713									6	-0.845	0.071	1.34
	SWJAT-1	9	0.792	0.019	4.69	9	0.756	0.030	39.8658												
	SWJAVS-1									9	-0.687	0.060	10.86	9	-0.707	0.050	4.07				
	SWMAVT-1									14	0.582	0.077	34.73	14	0.550	0.099	11.72				
	SWMJS-1									14	0.825	0.006	8.27	14	0.718	0.029	6.92				
	SWMJVT-1									14	-0.595	0.091	16.71	14	-0.710	0.032	7.09				
	SWSOT-1					12	0.656	0.054	55.52												
	VMWASN-1	26	0.580	0.006	27.00													26	0.427	0.054	31.49
Lag -1 Summary		**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		17	0.741	0.041	11.65	26	0.667	0.045	71.66	15	0.727	0.049	12.73	17	0.715	0.048	6.92	11	0.678	0.058	11.11

Appendix I. continued.

		Eastern Age 4				Northern Age 4				Montague Age 4				PWS Total Age 4				PWS R/S Age 4			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	CSJAS0									9	-0.825	0.006	10.82	9	-0.651	0.058	11.08				
	CSJAT0	9	0.624	0.072	13.53									9	0.757	0.018	8.20	9	0.888	0.040	12.82
	CSJAVT0													9	-0.587	0.097	12.59				
	CSMJT0									11	0.715	0.030	9.73								
	CSSOT0					11	0.659	0.038	41.07												
	CSSOVT0																	11	-0.635	0.048	18.73
	ENTJAS0									7	-0.953	0.003	3.75								
	ENTJAT0									7	0.777	0.069	16.15								
	ENTJAVT0																	7	-0.772	0.072	5.80
	ENTMAVT0									7	0.920	0.009	2.64								
	ENTMJT0									9	0.770	0.043	7.09								
	ENTSOT0	8	-0.742	0.056	12.06	8	0.715	0.070	17.87												
	ENTSOVS0																	8	-0.728	0.064	10.13
	GFEAJF0	26	0.523	0.015	41.09									26	0.465	0.034	33.88	26	0.569	0.007	32.64
	HSEAA0									26	0.664	0.001	42.71	26	0.547	0.010	30.38	26	0.487	0.025	37.94
	HSEAJF0									26	0.531	0.013	72.20	26	0.514	0.017	31.93	26	0.534	0.013	34.67
	JANAUW0					26	-0.448	0.032	148.26	26	0.436	0.037	92.33								
	MARAFWD0									26	0.609	0.002	71.80								
	MSJAT0	9	0.831	0.011	8.42	9	0.842	0.009	41.28					9	0.881	0.004	6.02	9	0.775	0.024	12.88
	MSJAVS0									9	-0.710	0.049	22.06								
	MSJAVT0	9	-0.752	0.031	11.83	9	-0.844	0.008	24.69					9	-0.768	0.026	11.06	9	-0.739	0.036	14.66
	MSMAT0	13	0.755	0.012	7.67	13	0.638	0.047	79.67					13	0.667	0.035	8.56				
	MSMJT0	14	0.605	0.064	26.74									10	0.635	0.049	9.77				
	MSSOS0									7	-0.762	0.078	5.35								
	MSSOVT0									7	-0.801	0.056	5.33								
	MWBAA0									26	0.580	0.006	50.43								
	MWBAJF0									26	0.551	0.010	70.04	26	0.479	0.028	33.40	26	0.508	0.019	35.98
Lag 0	MWAD0	27	0.533	0.011	39.09													27	0.509	0.015	35.72
	MWAJF0	26	0.659	0.001	32.02									26	0.545	0.011	30.51	26	0.661	0.001	27.29
	MWAMA0	26	0.537	0.012	40.23																
	NEMAT0					6	0.868	0.025	13.91												
	NEMJT0	5	0.932	0.068	4.27					5	0.926	0.074	1.73	5	0.938	0.062	2.39				
	NESOVS0	8	-0.653	0.087	15.40													3	-0.998	0.038	0.21
	NSJAS0									6	-0.745	0.089	13.25								
	NSJAT0					6	0.751	0.085	18.30												
	NSJAVT0					6	-0.892	0.017	3.47												
	NSMAT0					11	0.629	0.052	40.71												
	NSMJT0	12	0.698	0.037	17.68					12	0.664	0.051	29.71	12	0.793	0.011	8.26	12	0.728	0.026	14.91
	NSSOT0					8	-0.713	0.072	14.27												
	OCTAUW0													26	-0.443	0.034	35.54				
	PKZOOPA0					19	0.682	0.005	79.76												
	PWSJAT0									12	0.812	0.002	23.60	12	0.745	0.009	12.12	12	0.635	0.036	18.43
	PWSJAVT0	12	-0.596	0.053	18.27									12	-0.663	0.026	15.25	12	-0.647	0.031	17.95
	PWSMJT0	19	0.452	0.091	35.49					19	0.652	0.008	50.86	19	0.630	0.012	22.27	8	-0.624	0.062	5.01
	PWSMJVT0					19	-0.561	0.030	88.77												
	PWSSOT0					15	-0.662	0.012	56.44												
	SEJAT0									4	0.924	0.076	1.92	4	0.904	0.096	2.08				
	SEMAVT0									8	-0.703	0.078	9.66								
	SEMJVT0					9	0.699	0.074	21.23												
	SEPAUW0													26	-0.440	0.036	35.65	26	-0.455	0.029	39.72
	SWMAT0					14	0.721	0.012	42.68												
	SWMAVS0									14	-0.663	0.026	17.93								
	SWSOT0					12	0.618	0.057	45.79												
	VMWAA0									26	0.649	0.001	43.99	26	0.483	0.026	33.06	26	0.505	0.020	37.07
	VMWAJF0	26	0.484	0.026	43.30									26	0.486	0.026	33.14	26	0.556	0.009	33.55
Lag 0 Summary		**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		16	0.649	0.040	22.94	17	0.702	0.038	45.72	24	0.722	0.034	28.13	22	0.637	0.033	19.41	20	0.638	0.031	22.31

Appendix I. continued.

		Eastern Age 4				Northern Age 4				Montague Age 4				PWS Total Age 4				PWS R/S Age 4			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	APRAUW1	25	0.531	0.009	40.55																
	AVEZOOPA1	19	0.733	0.001	15.20	19	0.699	0.003	85.55					19	0.645	0.007	19.86	19	0.604	0.013	20.71
	CSJAS1									9	0.618	0.076	14.10	9	0.624	0.072	12.08				
	CSJAVT1									9	0.758	0.018	9.71								
	CSMAVT1	12	0.630	0.028	25.83					12	0.517	0.085	40.32	12	0.600	0.039	18.69	12	0.665	0.018	17.34
	CSMJT1	11	-0.582	0.077	19.10	13	-0.651	0.041	56.67	11	-0.624	0.054	19.73	11	-0.721	0.019	9.89	11	-0.631	0.050	11.74
	CSMJVT1	11	-0.863	0.001	7.39	11	-0.780	0.008	38.56					11	-0.838	0.002	6.14	11	-0.812	0.004	6.66
	CSSOS1									11	-0.598	0.052	36.77								
	CSSOVS1									11	0.708	0.015	28.56								
	DECAUW1																	25	-0.424	0.044	41.08
	ENSOSP1					26	-0.434	0.039	149.99					26	-0.426	0.042	36.17	26	-0.417	0.048	41.37
	ENTJAVS1					7	-0.870	0.024	11.78												
	ENTMAVS1					7	0.859	0.013	16.54					7	0.736	0.059	4.36				
	ENTMAVT1									7	-0.703	0.078	13.41								
	ENTMJVT1													9	-0.628	0.095	7.25				
	ENTSOVS1									8	0.664	0.073	29.40	8	0.747	0.033	5.16				
	ENTSOVT1	8	0.661	0.075	8.56																
	MSMJS1									14	-0.564	0.071	28.46								
	MSSOS1									7	-0.811	0.027	12.41								
	MWSAMA1									25	0.442	0.045	92.57								
	MWAJF1	25	0.502	0.020	41.18																
	MWAMA1																	25	0.501	0.021	37.00
	NEMAT1																	6	0.899	0.015	2.65
Lag +1	NEMJVT1	5	0.891	0.042	2.43																
	NESOVT1													3	0.995	0.063	0.11				
	NSSOS1	7	0.743	0.056	6.63																
	NSSOVT1									7	-0.868	0.011	13.46								
	PKZOOPA1	19	0.502	0.047	24.59	19	0.689	0.003	87.93												
	PWSJAVT1									12	0.754	0.007	21.78	12	0.634	0.036	12.47				
	PWSMAVT1	15	0.519	0.069	30.86									15	0.504	0.079	22.59	15	0.570	0.042	21.46
	PWSMJVT1	18	-0.442	0.099	23.45	18	-0.583	0.022	75.37												
	PWSSOS1									14	-0.625	0.022	41.27								
	PWSSOT1					14	0.483	0.094	78.87												
	PWSSOVS1									14	0.918	0.000	10.61	14	0.635	0.020	13.20	14	0.480	0.097	18.09
	SEJAS1	4	0.908	0.092	4.47					4	0.990	0.010	0.47	4	0.988	0.012	0.56	4	0.996	0.004	0.12
	SEJAVS1	4	0.904	0.096	4.68	4	0.943	0.057	8.72												
	SEJAVT1	4	0.994	0.006	0.30	4	0.975	0.025	3.93					4	0.908	0.092	4.19				
	SEMAS1	8	0.810	0.015	7.77	8	0.643	0.085	39.69					8	0.708	0.049	9.20	8	0.790	0.020	5.39
	SEMJVT1	9	-0.916	0.001	4.16	9	-0.824	0.012	28.99					9	-0.700	0.053	9.22	9	-0.691	0.058	8.65
	SESOS1	6	-0.824	0.044	6.29					6	-0.793	0.060	7.55	6	-0.814	0.049	6.86	6	-0.952	0.003	1.07
	SESOVS1	6	0.793	0.060	7.26	6	0.733	0.097	28.88												
	SWJAVS1																	9	-0.697	0.054	4.60
	SWJAVT1									9	0.731	0.040	7.60								
	SWMAT1	14	0.614	0.034	26.72									14	0.512	0.089	21.55	14	0.634	0.027	18.59
	SWMAVT1									14	-0.607	0.036	12.73								
	SWSOS1									12	-0.565	0.060	47.40								
	SWSOVS1									12	0.786	0.004	26.62	12	0.732	0.010	9.40	12	0.697	0.017	9.05
	VMWAD1																	26	0.431	0.045	38.77
Lag +1	**Summary**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		20	0.718	0.044	15.37	14	0.726	0.037	50.82	21	0.897	0.040	24.52	20	0.705	0.046	11.45	18	0.661	0.032	16.91

Appendix I. continued.

		Eastern Age 4				Northern Age 4				Montague Age 4				PWS Total Age 4				PWS R/S Age 4			
		n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC	n	r	p-value	AIC
	CSSOT2									11	0.716	0.013	32.00								
	ENTMAS2									12	-0.625	0.012	11.75								
	ENTMAT2																	7	0.702	0.079	12.53
	ENTMAVT2									7	-0.841	0.018	13.40								
	ENTMJS2																	9	0.685	0.061	12.53
	ENTMJVS2					9	0.669	0.064	16.04												
	ENTSOT2									8	0.824	0.012	21.69								
	JANAUW2	24	-0.509	0.013	41.68	24	-0.474	0.022	147.73					24	-0.567	0.005	30.01	24	-0.576	0.004	33.48
	JUNEAUW2	24	0.467	0.025	44.20																
	MSMAS2					13	0.547	0.052	50.55												
	MSMAVT2					13	-0.540	0.057	51.11												
	MSMJS2					14	0.781	0.003	24.05												
	MSMJVS2					14	-0.534	0.074	44.12												
	MW3AMJ2	25	0.578	0.005	36.50													25	0.560	0.007	33.81
	MWAD2	25	0.442	0.040	34.39																
	MWAMJ2	25	0.699	0.005	28.06									25	0.645	0.001	24.90	25	0.660	0.000	26.48
	NEMAVT2									6	0.758	0.081	19.39								
	NESOS2																	3	0.992	0.079	0.10
	NESOVS2	7	-0.423	0.033	19.15																
Lag +2	NSJAVS2	6	-0.842	0.035	6.63									6	-0.834	0.039	2.58	6	-0.863	0.027	3.45
	NSMJT2									10	-0.679	0.044	24.73								
	NSMJVS2					10	-0.594	0.071	18.69												
	NSSOVT2									7	-0.958	0.001	5.35								
	PWSJAVT-1					12	-0.534	0.090	78.67												
	PWSMAVT2	14	0.549	0.064	27.31																
	PWSMJS2					17	0.486	0.067	74.90												
	PWSMJT2									17	-0.482	0.069	46.35								
	PWSMJVT2	17	-0.462	0.083	28.61	17	-0.620	0.014	60.27												
	PWSSOT2																	14	0.568	0.034	22.39
	SEMAS2					8	0.652	0.077	21.99												
	SEMAT2									8	0.789	0.020	14.12								
	SEMJS2									9	0.785	0.012	13.97								
	SEMJVS2									9	-0.626	0.071	22.11								
	SWJAVT2					9	-0.867	0.005	22.26												
	SWMAT2	14	0.523	0.081	28.44									14	0.506	0.094	17.21	14	0.589	0.044	20.99
	SWMJS2					11	-0.651	0.030	44.90												
	SWMJVT2					13	-0.598	0.052	50.19												
	SWSOT2									12	0.543	0.068	41.52								
	SWSOVS2									12	0.528	0.077	42.42								
Lag +2 Summary		**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**	**# Var.**	**Avg |r|**	**Avg**	**Avg**
		10	0.549	0.038	29.52	14	0.611	0.053	50.39	13	0.704	0.038	23.75	4	0.638	0.035	18.67	9	0.691	0.037	18.42
Age 4 Summary		**63**	**0.680**	**0.041**	**18.54**	**71**	**0.676**	**0.043**	**57.14**	**73**	**0.713**	**0.040**	**23.15**	**63**	**0.680**	**0.041**	**13.47**	**58**	**0.661**	**0.037**	**17.90**

Appendix II. Results from the Principal Components PC) analysis for reduction of environmental variables. Listed are the sample size (n), standard deviation of each PC (equivalent to the square root of the eigenvalue), the proportion of variance explained by the PC, the variables included in the analysis, and the loadings, sometimes referred as the eigenvector of coefficients. To derive a PC variable, the loadings are used as coefficients in linear combinations of the normalized variables included in each PC. Only the PCs explaining 90% of the variance were used in the analysis. The codes for the variables are listed in Table 1.

Eastern Age 3

PC Variable	PC1 Wind	PC2 Wind	PC3 Wind		PC1 UW	PC2 UW	PC3 UW
n	15	18	15		23	23	23
St. Dev.	3.550	1.290	1.090		78.580	41.770	14.380
Prop. Variance	0.696	0.091	0.066		0.743	0.210	0.025
Variable		Loadings		Variable		Loadings	
MWAJF0	0.306	0.000	-0.161	JANAUW2	-0.421	-0.733	-0.533
MWAJF1	0.347	-0.325	0.125	FEBAUW2	0.816	-0.557	-0.116
MWAMA0	0.251	0.280	0.226	APRAUW2	0.000	0.000	0.000
MWAMA-2	0.394	0.000	-0.532	JUNEAUW2	0.000	0.000	0.000
MWAMA1	0.278	-0.179	0.000	SEPAUW0	0.000	0.000	0.000
MWAMJ-2	0.120	0.262	-0.321	DECAUW1	0.379	0.388	0.836
MWASN0	0.314	-0.243	0.000				
MWASN-1	0.315	0.000	0.227				
MWASN-2	0.291	0.000	-0.373				
MWAD0	0.425	0.103	0.558				
VMWAA0	0.115	0.000	0.117				

Northern Age 3

PC Variable	PC1 Climate		PC1 UW	PC2 UW	PC3 UW	PC4 UW
n	28		24	25	24	25
St. Dev.	3.150		112.090	90.416	62.711	48.811
Prop. Variance	0.911		0.445	0.290	0.139	0.085
Variable	Loadings	Variable		Loadings		
PMDOSP2	0.000	JANAUW2	0.544	0.000	0.140	0.000
PMDOSU2	0.000	JANAUW-1	0.206	-0.306	-0.927	0.000
PMDOWI2	0.000	FEBAUW-1	0.432	-0.774	0.332	-0.147
PIDOF2	0.000	FEBAUW-2	0.626	0.542	0.000	-0.373
PIDOSP2	0.000	SEPTAUW0	0.000	0.000	0.000	0.000
PIDOSU2	0.000	DECAUW1	0.284	0.108	0.000	0.910
PIDOW2	0.000					
PDOW-2	0.249					
ALPI-2	0.965					

Montague Age 3

PC Variable	PC1 Wind		PC1 FWD	PC2 FWD	PC3 FWD
n	24		26	26	26
St. Dev.	298.700		11919.324	7254.090	5034.830
Prop. Variance	0.912		0.646	0.239	0.115
Variable	Loadings	Variable		Loadings	
VMWAMA0	0.000	MARAFWD0	0.154	-0.630	0.761
VMWAA2	0.000	SEPAFWD-1	0.499	-0.615	-0.610
MW3AMA0	0.979	NOVAFWD-2	0.853	0.474	0.220
MW3AA0	0.205				
HSEAJF-1	0.000				
HSEAMA0	0.000				
HSEAA0	0.000				

Appendix II. Continued.

PWS Total Age 3

PC Variable	PC1 Wind	PC2 Wind	PC3 Wind		PC1 FWD	PC2 FWD
n	26	22	22		27	27
St. Dev.	2.658	2.010	1.003		11368.990	7794.500
Prop. Variance	0.570	0.326	0.081		0.680	0.320
Variable		Loadings		Variable	Loadings	
MWAMA-2	0.000	-0.768	-0.529	SEPTAFWD-1	0.304	0.953
MWAMJ-2	0.000	-0.317	-0.172	OCTAFWD-2	0.953	-0.304
VMWAMJ-2	0.000	-0.550	0.830			
VMWAA0	0.995	0.000	0.000			

PWS R/S Age 3

PC Variable	PC1 UW	PC2 UW	PC3 UW		PC1 FWD	PC2 FWD
n	23	23	23		25	25
St. Dev.	88.992	66.240			12961.630	8309.140
Prop. Variance	0.628	0.348			0.709	0.291
Variable		Loadings		Variable	Loadings	
JANAUW2	0.420	0.715	-0.543	OCTAFWD-2	-0.769	-0.639
FEBAUW2	0.795	-0.578	-0.151	NOVAFWD1	0.639	-0.769
MARAUW-2	-0.172	0.000	-0.396			
JUNEAUW2	0.000	0.000	0.000			
JUNEAUW-2	0.000	0.000	0.000			
SEPAUW2	0.000	0.000	0.000			
DECAUW1	0.386	0.383	0.722			
SEPAUW0	0.000	0.000	0.000			

PC Variable	PC1 Wind*	PC2 Wind	PC3 Wind
n	17	17	17
St. Dev.	**2.295**	1.415	0.628
Prop. Variance	**0.646**	0.246	0.048
Variable		Loadings	
MWAMA-2	**0.673**	-0.211	0.473
MWAMJ2	**0.115**	0.156	0.649
MWAMJ-2	**0.284**	-0.258	0.000
MWASN-2	**0.570**	-0.220	-0.576
VMWAA0	**0.357**	0.903	-0.153

*** PC used in the age-3 models, Table 5.**

Appendix II. Continued.

Eastern Age 4

PC Variable	PC1 Wind	PC2 Wind	PC3 Wind	PC4 Wind		PC1 UW	PC2 UW
n	15	16	18	17		24	24
St. Dev.	5.028	2.796	1.947	1.344		88.992	66.241
Prop. Variance	0.615	0.805	0.897	0.941		0.628	0.348
Variable	Loadings				Variable	Loadings	
MWAJF0	0.243	-0.101	0.159	-0.242	JANAUW-2	0.974	0.223
MWAJF1	0.189	-0.153	0.000	-0.189	JANAUW2	0.223	-0.972
MWAJF2	0.185	-0.162	0.000	-0.390	APRAUW1	0.000	0.000
MWAJF-2	0.346	-0.262	-0.174	0.000	JUNEAUW-2	0.000	0.000
MWAMA0	0.326	-0.108	0.119	0.000	JUNEAUW2	0.000	0.000
MWAMJ2	0.000	0.000	0.178	0.000			
MWASN-1	0.237	0.000	0.000	0.101			
MWAD0	0.149	0.000	0.000	0.000			
MWAD2	0.327	-0.282	-0.182	-0.376			
VMWAJF0	0.314	0.204	0.826	0.121			
VMWAMJ2	0.000	0.728	0.000	-0.629			
VMWASN-1	0.598	0.449	-0.395	0.414			

PC Variable	PC1 Wind2	PC2 Wind2	PC3 Wind2
n	18	18	19
St. Dev.	0.018	0.013	0.010
Prop. Variance	0.513	0.293	0.165
Variable	Loadings		
HSEAMJ2	-0.580	0.813	0.000
GFEAJF0	0.527	0.415	-0.339
GFEAMJ-2	0.000	0.000	0.000
GFEASN-2	0.361	0.227	0.904
GFEASN-1	0.505	0.338	-0.260

Northern Age 4

PC Variable	PC1 UW	PC2 UW	PC3 UW	PC4 UW		PC1 Climate	PC2 Climate	PC3 Climate	PC4 Climate
n	24	24	24	24		25	25	25	25
St. Dev.	110.808	76.314	72.030	56.398		0.946	0.615	0.383	0.340
Prop. Variance	0.417	0.198	0.176	0.108		0.575	0.243	0.095	0.074
Variable	Loadings				Variable	Loadings			
JANAUW2	0.318	0.324	0.369	-0.390	PDOW-1	-0.883	0.272	-0.360	-0.126
JANAUW0	0.117	0.438	-0.658	-0.560	PMDOF-2	0.156	0.000	-0.241	-0.259
JANAUW-1	0.303	0.350	-0.424	0.712	PMDOF2	0.135	0.114	-0.318	0.214
JANAUW-2	0.569	-0.728	-0.314	-0.143	PMDOSP-1	0.141	0.000	-0.174	-0.415
FEBAUW-1	0.685	0.226	0.390	0.000	PMDOSP-2	0.153	0.127	-0.305	0.000
					PMDOSP2	0.102	0.000	-0.282	0.364
					PMDOSU-1	0.126	0.000	-0.124	-0.439
					PMDOSU-2	0.155	0.116	-0.273	-0.153
					PMDOSU2	0.120	0.110	-0.297	0.299
					PMDOW-1	0.132	0.000	-0.155	-0.395
					PMDOW-2	0.151	0.105	-0.289	0.000
					PMDOW2	0.104	0.000	-0.290	0.317
					ENSOSP1	0.137	0.915	0.372	0.000

Appendix II. Continued.

Montague Age 4					
PC Variable	**PC1 MW3**	**PC2 MW3**		**PC1 Wind**	**PC2 Wind**
n	23	21		24	24
St. Dev.	359.668	253.564		0.074	0.030
Prop. Variance	0.625	0.311		0.861	0.140
Variable	**Loadings**		**Variable**	**Loadings**	
MW3AJF0	0.391	0.893	HSEAJF0	-0.976	0.216
MW3AMA1	0.920	-0.384	HSEAA0	-0.216	-0.976
MW3AA0	0.000	0.235			

PWS Total Age 4						
PC Variable	**PC1 Wind**	**PC2 Wind**	**PC3 Wind**		**PC1 UW**	**PC2 UW**
n	21	24	23		24	24
St. Dev.	3.189	1.511	1.035		88.954	66.183
Prop. Variance	0.739	0.166	0.078		0.624	0.345
Variable	**Loadings**			**Variable**	**Loadings**	
MWAJF0	0.428	0.000	0.737	JANAUW2	0.225	0.972
MWAMJ2	0.140	0.000	0.511	JANAUW-2	0.973	-0.228
VMWAJF0	0.824	-0.349	-0.432	SEPAUW0	0.000	0.000
VMWAA0	0.344	0.934	0.000	OCTAUW0	0.000	0.000

PC Variable	**PC1 Wind2**	**PC2 Wind2**
n	24.000	24.000
St. Dev.	0.074	0.030
Prop. Variance	0.851	0.137
Variable	**Loadings**	
HSEAJF0	0.970	-0.201
HSEAA0	0.213	0.974
GFEAJF0	0.119	-0.101

Appendix II. Continued.

PWS R/S Age 4

PC Variable	PC1 Wind	PC2 Wind	PC3 Wind	PC4 Wind		PC1 MW3	PC2 MW3
n	17	19	17	18		23	23
St. Dev.	3.802	3.414	1.677	1.284		277.774	124.451
Prop. Variance	0.431	0.347	0.084	0.049		0.833	0.167
Variable	Loadings				Variable	Loadings	
MWAJF0	-0.245	0.113	0.107	0.000	MW3AJF0	-0.984	0.180
MWAMA1	-0.165	0.000	0.387	0.154	MW3AMJ2	-0.180	-0.984
MWAMJ2	0.000	0.000	0.000	0.000			
MWASN-1	-0.178	0.149	0.000	0.000			
MWASN-2	-0.170	0.173	0.106	0.000			
MWAD0	-0.287	0.000	0.470	0.000			
VMWAJF0	-0.431	0.521	0.000	-0.591			
VMWAA0	0.000	0.238	0.507	0.484			
VMWASN-1	-0.182	0.502	-0.558	0.594			
VMWAD1	0.739	0.589	0.179	-0.167			

PC Variable	PC1 Wind2	PC2 Wind2		PC1 UW	PC2 UW
n	24	24		24	24
St. Dev.	0.076	0.030		77.015	42.917
Prop. Variance	0.857	0.131		0.747	0.232
Variable	Loadings		Variable	Loadings	
HSEAJF0	0.968	-0.210	JANAUW2	0.813	-0.577
HSEAA0	0.220	0.973	JUNEAUW-2	0.000	0.000
GFEAJF0	0.117	0.000	SEPAUW0	0.000	0.000
GFEAMJ-2	0.000	0.000	DECAUW1	0.573	0.813

PC Variable	PC1 ClimZoop	PC2 ClimZoop	PC3 ClimZoop
n	19	19	19
St. Dev.	1.239	0.728	0.549
Prop. Variance	0.649	0.224	0.127
Variable	Loadings		
AVEZOOPA1	-0.916	-0.211	-0.342
PDOSP-2	0.185	-0.977	0.109
ENSOSP1	0.357	0.000	-0.933

Appendix III. The variability in functional response of herring recruitment to environmental factors (Chapter 4, Table 1), for the year prior to year-class formation (lag –1), the cohort year (lag 0), and the second and third year of life (juveniles; lag +1 and +2), is shown as the number of negative versus positive correlations (# Neg. Corr., # Pos. Corr.) between recruitment response and lagged environmental predictor variables.

Variable Type	Time Period	Lag	# Neg. Corr	# Pos. Corr.
Climate	Mar-Apr (Spring)	-1	1	1
	Mar-Apr	1	4	0
	July-Aug (Late Summer)	-1	1	0
	Dec-Feb (Winter)	-1	1	1
	Dec-Feb	2	0	1
	Annual	2	0	1
Freshwater	Mar-Apr	0	0	2
	Sep-Nov (Fall)	-1	0	2
	Sep-Nov (Fall)	1	2	0
Mean Wind Speed	Mar-Apr	0	0	2
	Mar-Apr	1	0	2
	May-June (Early Summer)	2	0	4
	Sep-Nov	0	0	1
	Sep-Nov	-1	0	3
	Dec-Jan	-1	0	1
	Dec-Jan	0	0	7
	Dec-Jan	1	0	2
	Dec-Jan	2	0	1
Wind Mixing	Mar-Apr	0	0	1
	Mar-Apr	1	0	1
	May-June	2	0	2
	July-Aug	0	0	3
	Dec-Feb	0	0	3
Variance Wind Speed	Mar-Apr	0	0	1
	July-Aug	0	0	6
	July-Aug	2	1	0
	Sep-Nov	-1	0	2
	Dec-Feb	0	0	3
	Dec-Feb	1	0	1
Wind Events	Mar-Apr	0	0	1
	July-Aug	0	0	6
	Sep-Nov	-1	0	1
	Dec-Feb	-1	0	2
	Dec-Feb	0	0	6
	Dec-Feb	1	0	1
Zooplankton	Spr	0	0	3
	Spr	1	0	14
Upwelling	Mar-Apr	1	0	1
	Mar-Apr	2	0	1
	May-June	2	0	3
	Sep-Nov	0	6	0
	Dec-Feb	-1	4	0
	Dec-Feb	0	1	1
	Dec-Feb	1	4	0
	Dec-Feb	2	8	0

Appendix III. Continued.

Variable Type	Time Period	Lag	# Neg. Corr	# Pos. Corr.
SSS	Mar-Apr	-1	2	11
	Mar-Apr	0	2	0
	Mar-Apr	1	1	8
	Mar-Apr	2	1	3
	May-Jun	-1	1	12
	May-Jun	0	2	0
	May-Jun	1	4	1
	May-Jun	2	2	13
	July-Aug	-1	12	0
	July-Aug	0	7	0
	July-Aug	1	0	7
	Sep-Oct	-1	0	15
	Sep-Oct	0	5	1
	Sep-Oct	1	16	1
	Sep-Oct	2	2	3
SST	Mar-Apr	-1	6	2
	Mar-Apr	0	0	6
	Mar-Apr	1	0	18
	Mar-Apr	2	1	7
	May-Jun	0	1	17
	May-Jun	1	5	0
	May-Jun	2	5	1
	Jul-Aug	-1	0	19
	Jul-Aug	0	1	29
	Jul-Aug	1	6	0
	Sep-Oct	-1	0	4
	Sep-Oct	0	6	3
	Sep-Oct	1	0	7
	Sep-Oct	2	0	13
Variance SSS	Mar-Apr	-1	14	1
	Mar-Apr	0	1	0
	Mar-Apr	1	0	2
	Mar-Apr	2	0	3
	May-Jun	-1	11	3
	May-Jun	0	1	2
	May-Jun	2	6	1
	Jul-Aug	-1	7	0
	Jul-Aug	0	1	1
	Jul-Aug	1	2	6
	Jul-Aug	2	7	0
	Sep-Oct	-1	18	
	Sep-Oct	0	1	2
	Sep-Oct	1	0	24
	Sep-Oct	2	2	2
Variance SST	Mar-Apr	-1	8	8
	Mar-Apr	0	2	4
	Mar-Apr	1	5	15
	Mar-Apr	2	3	13
	May-Jun	-1	5	2
	May-Jun	0	5	2
	May-Jun	1	12	4
	May-Jun	2	8	0
	Jul-Aug	-1	11	1
	Jul-Aug	0	16	1
	Jul-Aug	1	0	15
	Jul-Aug	2	3	0
	Sep-Oct	-1	5	6
	Sep-Oct	0	3	0
	Sep-Oct	1	4	8
	Sep-Oct	2	2	0

Summary and Conclusions

The Opposing Response Theory

Results from this study, indicating that conditions positively impacting survival for one cohort may have deleterious effects on a cohort 1-2 years older or younger, led to a new theory explaining why strong successive year classes do not occur in northern Pacific herring populations. For several populations in the GOA, including PWS, strong year classes do not occur successively, rather every 3-7 years (Zheng 1996). From the results in Chapter 3, functional responses in recruitment to variables in a given season show a sign change, or opposing response, among lags that represent successive cohorts (Table 1). Ten out of the 43 possible combinations of variable type and season had sign changes (bolded in Table 1) between lags and 46% of the total significant environmental variables were included in those 10 combinations. The opposing responses observed occurred in spring, late summer and fall for freshwater and the local PWS oceanographic variables. For example in the fall, responses of herring recruitment to freshwater, salinity, and variance of salinity during the adult stage (-1 lag) were opposite to responses during the age-1 juvenile stage (+1 lag). Potential processes leading to this opposing response were discussed in Chapter 3 whereby mixing during the fall may result in stable oceanic salinity values, sustained summer SST values and sustained food supply for the adults residing in pelagic regions enhancing reproduction through improved adult condition. In contrast, excessive mixing in the nearshore nursery bays during fall may result in breaking down stratified layers that effectively "trapped" oceanic prey resources for juveniles in the surface waters where they feed. Another

opposing response example is during late summer when salinity is negatively and SST positively correlated to recruitment at age-0 (0 lag) but the opposite is true at age-1 (+1 lag). During late summer, when age-0 larvae recruit to nursery bays and undergo metamorphosis, sustained SST values and reduced salinity in pelagic surface waters and at the mouths of bays may equate to a continued presence of a mixed layer with oceanic food supplies concentrated near the surface for the young herring (from Chapter 3). In contrast, the age-1 herring already occupying inner regions of nursery bays may depend on regular and thorough mixing to breakdown the strong nearshore stratification acting as a barrier to the inflow of oceanic prey resources. Because juvenile herring overwintering survival depends on body condition in the fall (Foy and Paul 1999), availability of late summer food supplies is a critical factor for survival of young herring. Unfortunately, the same conditions that maintain food for age-0s in late summer may reduce food supplies for the age-1 juveniles and visa versa. The end result of these opposing responses would be extrinsic control of successive strong year classes.

The inclusion of a string of sequential ocean conditions, during critical life history periods, as a state variable may improve recruitment models. In this study, recruitment models were greatly improved with the addition of environmental variables. However, many variables during multiple critical life history periods were important. Assuming the theory of opposing response is correct, the temporal pattern of strong year classes reflects an environmental pattern of sequential ocean conditions conducive to stage-specific survival for each strong cohort and deleterious for weaker ones. The inclusion of this pattern of conditions for the critical survival periods identified in

Chapter 3 should result in improved recruitment models over inclusion of only one or two key variables. This pattern would be represented by a state variable incorporating an integrated series of specific ocean conditions as opposed to a simple continuous variable. In this case, logistic or factor level modeling may be more appropriate than traditional regression models.

Stage Specific Effects on Population and Recruitment

Population level and life stage-specific hypotheses, addressing stock structure and processes affecting year class formation, were listed in Chapter 1 and many were directly or indirectly tested in this study.

Population Level

Although the coherence of the Northern Gulf of Alaska (NGOA) herring population with climatic indices led to support for alternative H_a1 (population level is determined by an accumulation of bottom-up forcing and is mainly climate-driven), population regulation by top-down effects (null hypothesis) could not be ruled out. The null hypothesis was stated as:

H_n1. Population size is event-driven and determined by mainly top-down events such as disease outbreaks, increases in large predators (e.g. whales or sharks) or anthropogenic causes (e.g.overfishing, oil spills).

In Chapter 2, long-term population trends were significantly correlated with climate indices. In addition, growth in adult herring exhibited decadal scale oscillations and followed trends in zooplankton densities, a parameter heavily influenced by climatic trends (Brodeur and Ware 1992). The recruit per spawner index, a measure of herring

production, was also correlated with zooplankton and an east to west shift in the main spawning area. Although effects on recruitment from fishing mortality were explored and found to have no impact, natural predation was not directly addressed in this study and could have important population regulation effects. However, effects from predation could be masked if predation rates act in concert with climatic effects (e.g. low zooplankton equates to low growth and high mortality from predation). High potential predation risk exists in PWS with the presence of a large walleye pollock (*Theragra chalcogramma*) population that consumes a large number of juvenile salmon, juvenile herring and other locally abundant fish (Willette et al. 2001). There are also large numbers of piscivorous marine mammals residing in PWS year around. Reports of predator effects on Pacific herring are rare and vary in results. Herring recruitment models in British Columbia were improved with the inclusion of Pacific hake (*Merluccius productus*) biomass (a herring predator; Ware 1995) and there was also a weak effect on herring production by coho salmon (*Onchorhynchus kisutch*) predation (Schweigert 1996). The complex degree of behavioral responses, species interactions, and other external factors make it difficult to quantify predation rates. It is possible that at low population levels, the PWS population is in a "predator pit" (Walters and Juanes 1993; Hilborn and Mangel 1997; Chapter 1) that occurs when a reduced population results in smaller schools and fewer aggregations distributed over a smaller geographic range than at higher population levels. In this situation, herring are forced to spend more time at the edges of schools increasing predation risk and a stable or increasing predator population concentrates in the reduced geographic range resulting in an overall increase

in predator removals of herring. The existence of a predator pit would provide an explanation for the lack of a strong or even moderate year class since 1992, despite the 7 yr maximum period between strong year classes observed historically in PWS (Zheng 1996). An alternative explanation is that the population is at or near the minimum spawn threshold required to produce a year class. However, that is unlikely as a moderate year class resulted from the lowest population level ever observed in 1994 in PWS. In 1976, when PWS population levels were similar to the present, an extremely strong year class occurred. The inclusion of predation information in the recruitment model may become increasingly important if recruitment failure continues.

Adults

The model fits and numbers of –1 lagged environmental variables in recruitment models led to a rejection of the null hypothesis (H_n2 size-at-age of adults and behavioral choices during reproduction are not related to year-class size) and acceptance of the alternative (H_a2 environmental factors affecting size-at-age and behavioral choices of adults during reproduction also affect year-class formation, evident as correlations between year-class strength and factors occurring a year or more prior to spawning). In Chapter 1, I concluded that the main impacts on year-class formation during the adult stage originate in processes affecting reproductive rates, egg size, and characteristics of spawn deposition that carry on to future stages. These are mainly the adaptive, behavioral reproductive choices by adult herring that tend to optimize survival of offspring. Two of the eight critical periods defined in Chapter 3 occurred during the adult stage prior to the cohort year and local oceanic conditions (SST, salinity, and

variance of the two) were most deterministic of recruitment success for these periods. The optimal oceanic conditions listed in Chapter 3 during late summer and fall probably enhanced recruitment via better condition of adults, increased lipid storage in eggs and thus size at hatch, enhanced egg and yolk-sac larvae survival, and a good spatial overlap in time and space of larvae with food.

Embryo

Because conditions during the spawning through hatch and early larval stage (spring and early summer 0 lag) were less deterministic of recruitment strength than conditions prior to spawn (-1 lag), the alternative hypothesis for the embryo stages appears more appropriate than the null. Results from this study support the alternative hypothesis (H_a3 cumulative effect of adult size-at-age, adult behavioral choices during reproduction, and environmental conditions during incubation more deterministic of year-class strength than egg survival) over the null (H_n3 output of egg-larval survival models is correlated to year-class strength of the cohort modeled). Because there were significant variables with AIC scores lower than 10 (the best-fit criteria from Chapter 3) during the spring and early summer 0 lag period, processes during spawn, incubation and hatch cannot be completely ignored. During this period, recruitment was positively correlated with March freshwater discharge, March-April wind speeds, wind mixing and wind events, peak and average zooplankton production, and March-June SST but negatively correlated to March-June salinity, variance of March-June salinity, and variance of SST (Table 1). Anomalously high numbers of wind events and freshwater discharge might negatively impact egg survival via increased *in situ* mortality and

removals. However, these two variables were positively correlated to recruitment and, in combination with the other key variables, seem more likely to impact stratification and availability of food for emerging larvae. Given that the –1 lag variables produce better model fits, it is likely that effects on recruitment from spring-early summer processes are cumulative with the apparently more important processes during the adult stage that affect lipid reserves at hatch, size at hatch, spawn location (impacting the launch site for larvae), spawn timing, and the numbers of larval cohorts (batches). The predictive capabilities of currently available embryonic survival models would be improved by adding components to predict spawn timing, egg lipid reserves, larval size at hatch, an index of hatch cohort spatial patchiness, and a predator abundance index (e.g. magnitude of concurrent jellyfish bloom).

Larvae - Metamorphosis

Given the relative importance and model fit of variables during the larval drift stage (early summer 0 lag) was secondary to variables during metamorphosis (late summer 0 lag), adult (-1 lags) and juvenile stages (fall 0 lag, +1 and +2 lags), I concluded that reproductive behavior and adult condition at spawn has profound affects on larval survival and should be included in larval models along with processes during metamorphosis. I could not test the larval hypotheses posed in Chapter one. Mortality during larval drift is very high (Norcross and Brown 2001), despite adaptive adult reproductive behavior that provides compensatory mechanisms. Adult adaptive behavior includes timing spawn so eggs hatch when larval food is availability during oceanographic periods facilitating retention and distributing spawn in such a way that

larvae hatch in batches creating patchiness in larval distribution that may reduce overall predator encounter rates (Chapter 1). High mortality results from mainly jellyfish encounters, other predation, and advection away from suitable nursery habitat (Chapter 1). If larvae undergo metamorphosis in open water away from a dark shoreline, increased visibility caused by pigmentation coupled with poor swimming capabilities may result in heavy losses by predation. Larval drift simulation models produce reasonable replications of where larvae go, but do not include adult parameters that affect spawn timing, spawn distribution, and adult condition (as it affects larval condition). In addition, the existing models do not include parameters that represent larval survival rates during drift or at metamorphosis. Adding parameters including initial larval size or condition (or an adult proxy for that variable), spatial patchiness (or a spawn distribution and timing proxy), realistic larval vertical movements, boundary conditions (based on mixed layer depths and vertical temperature profiles), and proxies for food and predators could drastically improve models. Larval studies are generally expensive. Simulation models could provide a cost-effective alternative for studying larval processes and focus ship research on obtaining validation data.

Juvenile

The identification of critical periods occurring during the juvenile stage and the geographic diversity in responses of local age-3 and –4 recruitment to local environmental underscored the importance of spatially varying processes, occurring during this stage, to year class size regulation. Five of the 8 critical periods occurred during the juvenile stage and one period spanned the larvae to juvenile stages. During

these periods, the key processes identified were mainly effects of ocean conditions on food supply for the age-0 to -1 juveniles in the nearshore surface waters of the nursery bays and conditions at or near the mouths of nursery bays where age-0 recruits enter and age-2 immature herring exit. In PWS, the spatial variability in ocean conditions observed at nursery bays (Gay and Vaughan 2001) probably leads to the variability of growth, condition and survival observed (Norcross et al. 2001; Figure 1). Year-class strength may depend in part on the proportion of nursery bays and localities with optimal conditions during the critical periods. Given the variability observed among bays, the assumption that a single bay represents overall regional survival is flawed. However, in PWS, the results of this study indicate that ocean conditions in Eastern PWS may be more critical than conditions elsewhere. To better understand the role of spatial variability and proportion of "good" versus "bad" nursery habitat, ocean condition data from a larger number of sites would be required to feed ecosystem-based models and to answer why conditions in Eastern PWS appear important to PWS recruitment as a whole.

Although the hypotheses concerning regulation of year-class strength during the juvenile stage (Chapter 1) could not be specifically tested, the results from this study generally support some of the ideas posed on regulatory processes and underscore the deterministic importance of this life stage. From Chapter 3, age-3 recruitment was thought to present the proportion of the cohort maturing, rather than the size of the cohort. In addition, spring zooplankton at age-1 and ocean conditions during late summer and fall for age-1 to –2 juveniles were important explanatory variables in the

models. These results support the idea in H_a2, Corollary 2 (environmental conditions favorable to growth from age1 to 3 and condition of age 1 herring determine the proportion of age 3 herring spawning in a given cohort).

The importance of local and spatially varying ocean conditions during the juvenile stage in year class size determination provides support for H_n19 (growth and condition of juvenile herring dependent on site-specific factors that determine habitat quality) and underscores the importance of herring nursery habitat to recruiting processes. Finally, the identification of late summer +2 lag as a critical period provides some support for the ideas in H_a20 (recruitment of age-2 herring is dependent on intersection rate with adult herring and the probability of intersection is dependent on habitat conditions, timing of exit, juvenile condition or body size, and distribution of adults). The results from Chapter 3 indicated that increased mixing and ocean currents might interfere with the adult "joining" process by either creating a barrier for juveniles and/or by changing the distribution of adults.

The inability to formally test juvenile stage hypotheses results from the paucity of data available and difficulties in formulated and validated simulation models. The paucity of data problem is exacerbated by the increase in complexity over earlier life stages of biological interactions with the environment and behavioral responses. The only realistic method for testing hypotheses is probably simulated ecosystem-based models. However, because of the complexity of ecosystem-based models, the large number of poorly understood inputs at the juvenile stage, and the high cost of data

collection, validation of juvenile stage models will probably have to rely on data from only one or two case studies if any at all.

Metapopulation Theory for PWS

The results of this study support metapopulation theory posed in Chapter 1 stating that the PWS herring population comprises two well-defined local populations (Eastern and Southwestern) and a third less well-defined group (Northern). Furthermore, I suggested that strong year classes can only be formed in the southwest with a combination of favorable environmental conditions and eastern-northern migrants. The alternative hypothesis was that spatial complexity is solely a function of population size. If the alternative was correct, I concluded that recruit per spawner (R/S) ratios should decline with population size. However, there was not a significant effect of spawner population size on recruitment (Chapter 2). In contrast, R/S production declined in concert with changes in regional spawning, specifically the decline of Eastern area spawn (Chapter 2). In addition, recruitment to the hypothetical local population regions (Chapter 1) varied in response to environmental forcing (Chapter 3). Survival from age 0 to 1 also varied among regions in three out of the four years observed (Figure 1). A formal test of the metapopulation theory for PWS requires more definitive proof potentially including microsatellite DNA (expanded from O'Connel et al. 1998), otolith chemical markers (e.g. Campana et al. 1994), and/or a tagging study (see review by Hay et al. 1999) to track fidelity of spawners to local regions and the joining process of age-2 immature herring with adult aggregations.

The depressed herring population in PWS is not likely to rebound without spatial diversity in the local population structure. A strong year class has not occurred in PWS since 1992 (Chapter 3). Survival probability may be increased only with diverse spawning locations and a distribution of recruits occupying a high proportion of nursery habitat with favorable ocean conditions described earlier and in Chapter 3. Restricting the population to one locality (e.g. southwestern PWS) where population building is dependent on another locality (e.g. eastern PWS), due to regional metapopulation structure, may result in a continued depression of the population as a whole. Management objectives for Pacific herring should include provisions for maintaining spatial diversity whether stock structure is well defined or not (see Stephenson 1999). Over fishing a locality potentially important to regional population building is risky and irresponsible.

Applicability of Results

Although this study is mainly focused on a single population of Pacific herring, the findings are applicable to other herring populations and ecologically important species with similar life histories. The conceptual model (Chapter 1) summarizes an extensive knowledge base for Pacific herring and is therefore common to herring in general. The model is also applicable to other age-structured, beach spawning, fat-storing forage fish species, such as capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus*). Some minor modifications would render it applicable to eulachon (*Thaleichthys pacificus*), an anadromous species, but otherwise similar to the rest. All of these species are small, mature rapidly (compared to other marine species),

occupy habitats with a high degree of variability, have population responses large in amplitude that adhere to climatic trends and environmental regime shifts, and require annual or biannual assessments because of intermittent, unpredictable recruitment (King and McFarlane 2003). For herring, much of the information needed to parameterize an ecosystem-based was reviewed in Chapter 1 and the analysis in Chapter 3 defined focus points, in terms of times, seasons, and places that are most critical for year class formation. For the other three species, there is a general paucity of information compared to herring. Yet the decline in abundance of forage species, especially capelin, after a regime shift in the late 1970's (Anderson et al. 1997; Anderson and Piatt 1999), has been cited as a possible contributing factor of the substantial and unexplained declines of some sea birds, pinnipeds and other cetaceans in the North Pacific (Merrick et al. 1987; Piatt and Anderson 1996). Simulation modeling may be the only choice available to examine processes affecting recruitment and population building for these other species. Starting with known herring values and focusing modeling efforts on hypothesized critical life periods, parameters and algorithms are replaced when species-specific or more appropriate values become available.

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Table 1. The sign (positive or negative) and number of significantly correlated environmental variables to herring recruitment categorized by type of variable and season for each of the lags (-1, year prior to year-class formation; 0, eggs to juvenile stage age-0; 1, the second year of life or age-1; and 2, age-2 juvenile to immature adults). Also shown are the total number of variables under each category, the total number of positive versus negative variables for each lag, the total number of variables and the percent of variables involved in opposing response among lags (bolded and highlighted items).

		Lag				Total No.
Variable Type	**Season**	**-1**	**0**	**1**	**2**	**Variables**
Climate	Annual				+1	1
	Spring	-1,+1		-4		6
	Late Summer	-1				1
	Winter	-1,+1			+1	3
Freshwater	Spr		+2			2
	Fall	**+2**		**-2**		**4**
Upwelling Index	Spring			+1	+1	2
	Early Summer				+3	3
	Fall		-6			6
	Winter	-4	-1,+1	-4	-8	18
Gale Force Wind Events	Fall	+1				1
	Win		+3	+1		4
High Speed Wind Events	Spring		+1			1
	Late Summer		+6			6
	Winter	+2	+3			5
Mean Wind Speed	Spring		+2	+2		4
	Early Summer				+4	4
	Fall	+3	+1			4
	Winter	+1	+7	+2	+1	11
Wind Mixing	Spring		+1	+1		2
	Early Summer				+2	2
	Late Summer		+3			3
	Winter		+3			3
Variance of Wind Speed	Spring		+1			1
	Late Summer		**+6**		**-1**	**7**
	Fall	+2				2
	Winter		+3	+1		4
Salinity	Spring	-2,+11	-2	-1,+8	-1,+3	28
	Early Summer	-1,+12	-2	-4,+1	-2,+13	35
	Late Summer	**-12**	**-7**	**+7**		**26**
	Fall	**+15**	**-5,+1**	**-16,+1**	**-2,+3**	**43**
SST	**Spring**	**-6,+2**	**+6**	**+18**	**-1,+7**	**40**
	Early Summer		-1'+17	-5	-5,+1	29
	Late Summer	**+19**	**-1,+29**	**-6**		**55**
	Fall	**+4**	**-6,+3**	**+7**	**+13**	**33**
Variance of Salinity	**Spring**	**-14,+1**	**-1**	**+2**	**+3**	**21**
	Early Summer	-11,+3	-1,+2		-6,+1	24
	Late Summer	-7	-1,+1	-2,+6	-7	17
	Fall	**-18**	**-1,+2**	**+24**	**-2,+2**	**49**
Variance of SST	Spring	-8,+8	-2,+4	-5,+15	-3,+13	58
	Early Summer	-5,+2	-5,+2	-12,+4	-8	38
	Late Summer	**-11,+1**	**-16,+1**	**+15**	**-3**	**47**
	Fall	-5,+6	-3	-4,+8	-2	28
Zooplankton	Spring		+3	+14		17
Total Negative Correlations		107	61	65	51	284
Total Positive Correlations		97	114	138	72	421
Total Number Variables						**705**
Percent Involved in Opposing Response						**46.1%**

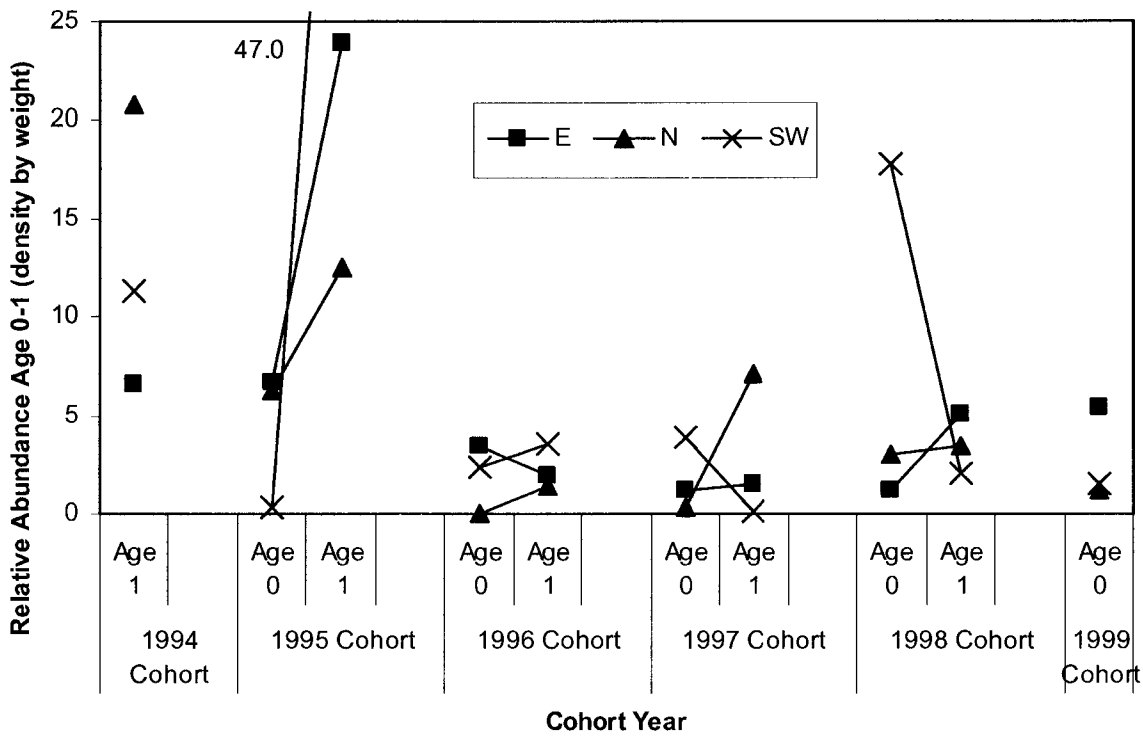

Figure 4.1.Relative abundance of age-0 to age–1 juvenile herring in three main regions of Prince William Sound, Alaska: Eastern (E), Northern (N), and Southwestern (SW) from 1994 to 1999. Abundance units are m^2 surface area of herring schools per km^2 area surveyed; surface area of schools is directly correlated with the biomass of the schools (Brown and Moreland 2000; Pitcher et al. 1985). Increases in biomass from age-0 to 1 probably represent cumulative growth and decreases mortality.